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mollusks in peril 2016 forum

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The first two artieles in this issue derive from the presentations given at the *Mollusks in Peril 2016 Forum*. The Forum took place at the Bailey-Matthews National Shell Museum on May 22–24, 2016, and encompassed hour-long presentations by eleven specialists in conservation, systematics, and ecology of mollusks. The subjeets spanned a broad range of subjects that ineluded Paeifie island land snail conservation, threats to pelagic mollusks, freshwater mollusks in peril, and ocean aeidifieation impacts on larval growth. The two papers presented here cover an update to reeent global estimates of extinct and endangered mollusks (Cowie, Régnier, Fontaine, and Bouehet) and an assessment of the impacts of mining on deep-sea mollusks (Sigwart, Chen, and Marsh). I want to thank Shell Museum Exeeutive Director and Forum co-organizer Dorrie Hipschman and major sponsors Smoky and Stephanie Payson for their enthusiasm and hard work. *Mollusks in Peril* will continue with a special session to bc held at the upeoming meeting of the American Malacologieal Society (July 16–21, 2017), at the University of Delaware (http://www.delmnh.org/ams2017).

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Measuring the Sixth Extinction: what do mollusks tell us?

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ABSTRACT

The International Union for Conservation of Nature (IUCN) is the premier global biodiversity conservation organization. Its *Red List* is a rigorous vehicle for assessing the conservation status of plant and animal species. However, although all animal and bird species recognized by IUCN have been evaluated, only a tiny fraction of invertebrates have been evaluated. As a measure of the numbers of extinct species (since around the year 1500) the *Red List* is probably quite accurate for birds and mammals, but severely underestimates the numbers for invertebrates. Nonetheless, molluscs stand out as the major group most severely impacted by extinction, with 297 of the 744 animal species listed as extinct in the third issue of the 2016 *Red List*. Here we review efforts to obtain a more realistic, albeit less rigorous, assessment of the numbers of extinct mollusk species. Our approach has been based on bibliographic research and consultation with experts, rather than following the highly detailed but restrictive IUCN *Categories and Criteria*. In 2009, this led to an assessment that 533 mollusk species were extinct, far more than the number on the *Red List*. In the present study we revisited this approach and here list 638 species as extinct, 380 as possibly extinct, and 14 as extinct in the wild, a total of 1,032 species in these combined categories, and more than twice as many as listed by IUCN in these categories. However, this approach only considers species for which information is available; it is therefore biased. In a study published in 2015 we developed an alternative approach, based on a random global sample of land snails, and estimated that 3,000–5,100 mollusk species have gone extinct. We review the main reasons for these extinctions: habitat destruction, impacts of introduced species, exploitation and collecting, and, potentially, climate change, and discuss relevant case studies. Oceanic island land snails, especially those of Pacific islands, have suffered the greatest proportion of the extinctions, with some species having gone extinct before being discovered and described scientifically. The Amastridae, an endemic Hawaiian family of 325 recognized species, may have lost all but 18 species. We outline the phases in this catastrophe: 1) pre-human and/or prehistoric extinction, either natural or anthropogenic, with species known only as fossils/subfossils; 2) extinction due to habitat destruction and introduction of a number of alien species by Pacific island people as they settled the islands; 3) extinction due to extensive habitat destruction and introduction of highly destructive invasive alien species following colonization by Westerners; 4) extinction following the advent of large-scale agriculture at the end of the 19th Century, at the time of a major increase in the land snail extinction rate globally; 5) extinction due to increased military activity, tourism, commerce, urbanization and the concomittant rapidly increasing introduction of invasive species after the Second World War. Extrapolating from our assessments of mollusks, we estimate that approximately 7.5–13% of all species have gone extinct since around year 1500. This is orders of magnitude greater than the 860 (0.04% of 2 million) listed as extinct by IUCN (2016). The biodiversity crisis is real.

Additional Keywords: Amastridae, biodiversity crisis, bivalves, *Euglandina*, Gambier Islands, Hawaii, IUCN, *Melanopsis*, Mollusca, non-marine, *Powelliphanta*, *Rhachistia aldabrae*, *Red List*, snails

INTRODUCTION

Over a decade ago, Lydeard et al. (2004) published a key paper outlining the decline of non-marine mollusks, the threats they face, and the high level of extinction compared with other major animal groups that had been documented as of 2002 by the International Union for Conservation of Nature on its *Red List*. The *Red List* program was initiated in 1964 and mollusks were first included in it in 1983, when 28 species were listed as extinct (Wells et al., 1983). The *Red List* only considers extinctions in modern historical times, from around the year 1500. Following the realization that an ill-conceived biological control program had caused the extinction in the wild of the entire fauna of partulid tree snails on the island of Moorea in French Polynesia (Murray et al., 1988), more effort was put into documenting mollusk extinctions on the *Red List*. A Moorean partulid appeared on the front cover of the 1990 *Red List* (IUCN, 1990), and when the 1994 *Red List* (Groombridge, 1994) was published, 255 species were listed as extinct. The number has gradually increased and the most recent *Red List* (IUCN, 2016) lists 297 mollusks as Extinct out of a total of 860 extinct species listed.

If we accept a figure of 2 million described species (Chapman (2009) estimated 1.9 million, and IISE (2017) documents a current yearly increment of around 18,000 newly described species; the *Red List* accepts 1,736,081 species), this means that between one and two species

have gone extinct per year since 1500, the year from which IUCN starts counting, or about 0.8 species extinctions per million species years (E/MSY). The background rate, based on the fossil record, is around 0.1–2.0 E/MSY (Ceballos et al., 2015). That the rate documented by IUCN is within the estimated range of the background rate has provided support for the suggestion by environmental skeptics (e.g., Lomborg, 2001) that there is no "Biodiversity Crisis", despite the views of many scientists and the media publicity surrounding the notion of the "Sixth Extinction", caused by human activities (Novacek, 2001; Leakey and Lewin, 1996). So the question becomes, is there really a crisis or is it a false or exaggerated claim by environmental activists and scientists with an arguably political agenda?

The key question to ask in trying to resolve this conflict is: how accurate really are the IUCN extinction data? This review summarizes the approaches that have been developed since the review of Lydeard et al. (2004) and that have attempted to begin to answer this question (Régnier et al., 2009, 2015a). It updates the assessments of Régnier et al. (2009) and reviews a case study of a Hawaiian land snail family, the Amastridae, that used these new approaches to obtain a realistic assessment of extinction (Régnier et al., 2015b).

IS THE IUCN RED LIST APPROPRIATE FOR ASSESSING EXTINCTION RATE?

The IUCN has assessed 85,604 species (IUCN, 2016). This represents a huge amount of detailed work by dedicated biologists, but nonetheless represents only 4.3% of the total 2 million animal and plant species. Although a small sample of overall biodiversity, if it were a random sample, some confidence could perhaps be placed in its assessment of extinction rate. However, it is not a random but a highly biased sample.

IUCN (2016) estimated that there are 5,567 known mammal species and 11,121 known bird species, total 16,688, although Chapman (2009) estimated 5,487 and 9,990, total 15,477, probably a result of differing taxonomic treatments and estimation protocols. IUCN (2016) has assessed all mammal and bird species that it recognizes. Of these, only 849 ($\sim$ 5%) were placed in the IUCN category "data deficient", that is, they lacked sufficient information to assess their conservation status according to the *IUCN Red List Categories and Criteria* (IUCN, 2012). Thus, the number of extinctions (239) listed for mammals and birds by IUCN (2016) is probably quite accurate.

However, the situation is very different for invertebrates, which constitute > 95% of described animal diversity, about 1.31 million (IUCN, 2016) or 1.5 million species (1.36 million of Chapman (2009) extrapolated by an annual increment of 1%). Only 18,609 of these species have been assessed, 1.2% of the total, with 7,205 (39%) of these deemed data deficient. Why is this? There are two main reasons: 1) taxonomic bias, and 2) the related relative difficulty of obtaining adequate data to assess the conservation status of invertebrates compared to vertebrates according to the IUCN criteria.

Taxonomic Bias

There are on average many specialists able to assess the conservation status of each mammal or bird species. As most mammal and bird species have been discovered and described, these specialists are primarily field biologists working on ecology, population biology, behavior, etc. In contrast, most invertebrate specialists are taxonomists or systematists (in the broad sense including those studying biogeography, phylogenetics, and the assessment of biodiversity), and most of these systematists each deal with tens to hundreds of species. There are roughly equal numbers of specialists focused on vertebrates, on plants and on invertebrates, yet plant species are roughly ten times, and invertebrates a hundred times, more numerous than vertebrates (Gaston and May, 1992; May, 2011).

This bias and the 100-fold greater relative number of vertebrate specialists compared to invertebrate specialists is reflected in the numbers of IUCN Species Survival Commission Specialist Groups focused on particular taxa: 73 for vertebrates and only 12 for invertebrates, with only one for the entire phylum Mollusca (Table 1). In contrast, many of the vertebrate Specialist Groups are focused on just one or a few species (e.g., African elephant, hyaenas, vultures, pelicans, etc.).

IUCN Criteria

The IUCN criteria are detailed and complex. They include precise quantitative determinations of remaining numbers of individuals, life history details, area occupied,

Table 1. Number of IUCN Specialist Groups for animals.

Vertebrates	No. of Groups	Invertebrates	No. of Groups
Mammals	35	Insects	4
Birds	16	Other arthropods	3
Reptiles/amphibians	12	Coral	1
Fish	10	Mollusks	1
		Geography/habitat	3
Total	**73**	**Total**	**12**

trends in abundances and range and many other parameters that are precisely defined. This detail and precision was developed by IUCN in response to criticism that its assessments were too qualitative and subjective, indeed secretive (e.g., Mrosovsky, 1997). All mammal and bird species have been evaluated based on these stringent criteria, with very few species considered Data Deficient. This has been possible because, as explained above, there are many specialists in the field generating the kind of data that are required.

In contrast, for the great majority of invertebrate species, few data relevant to the IUCN criteria exist other than what are available in the original descriptions (type localities and little else) and perhaps a small number of subsequent publications. Most of the field research of any relevance is undertaken as part of biodiversity inventories, the discovery and subsequent description of the vast number of species as yet unknown to science, or indeed to humanity.

MOLLUSKS ASSESSED BY IUCN

The most careful estimate of the number of described mollusk species (Rosenberg, 2014) suggested that there are 70,000–76,000, although IUCN (2016) estimated 85,000, following Chapman (2009). Compared to other invertebrate groups, a relatively high proportion of mollusk species has been assessed: 7,276 species (IUCN, 2016), or roughly 8.5–10%. However, in contrast to mammals and birds, a high proportion of these species was assessed as Data Deficient (2,463 species, 34%), for lack of adequate information addressing the IUCN criteria.

The *Red List* (IUCN, 2016) lists 860 species (744 animals, 116 plants) as Extinct, including 297 mollusk species. Mollusks, despite the small proportion of them that has been assessed, thus represent 35% of all species extinctions and 40% of animal extinctions, as reported by IUCN.

ALTERNATIVE APPROACHES TO ASSESSING MOLLUSK EXTINCTIONS

Régnier et al. (2009)

Given the shortcomings of the *Red List* in assessing the level of extinction of invertebrates overall, alternative approaches have been sought. Régnier et al. (2009) re-evaluated mollusk species listed as Extinct on the *Red List* of 2007 based on a review of the literature and by asking a cadre of biologists with expert knowledge to provide their opinion on the veracity of the *Red List* assessments. This literature review and gathering of expert knowledge also identified additional species not on the *Red List* but either documented in the literature as extinct or simply known to the experts as extinct. Some of the species listed as extinct were considered in fact not to be so, either because they had been found alive since being listed, or because they had been synonymized with extant species; and two species were excluded as being *nomina dubia*. Despite this reduction, from 302 species listed to 269 considered in fact to be extinct, overall the number of species considered extinct (both listed and not) increased to 533, including those considered Extinct in the Wild (13) and those considered "possibly extinct" (71) (Régnier et al., 2009: Supporting Information online), roughly twice as many as correctly considered Extinct on the *Red List*. Régnier et al. (2009) also listed 33 subspecies (including 5 extinct in the wild and 1 possibly extinct), for a total of 566 taxa.

Update of Régnier et al. (2009)

Following the same approach as that of Régnier et al. (2009), i.e., literature search and expert consultation (see the Acknowledgements for the names of the experts who provided information), we have updated the list of species considered extinct. We took the most recent evaluation of each species as representing its current status, which was either the most recent IUCN evaluation as listed in the *Red List* (IUCN, 2016), Régnier et al. (2009), or our own literature/expert consultation. We excluded species listed as Extinct, Possibly Extinct, or Extinct in the Wild on the *Red List* and/or by Régnier et al. (2009) if they are now thought to be extant (Appendix Table A1). We also did not consider subspecies, neither those recognized in the *Red List* nor those listed by Régnier et al. (2009). Subspecies and synonyms that have been recognized in the literature subsequently but that are still retained as valid species on the *Red List*, as well as undescribed species listed with provisional names on the *Red List*, were also excluded (Appendix Table A2).

Of the 297 species listed as Extinct on the *Red List*, we considered six as now only Possibly Extinct, three as Extinct in the Wild, 20 as extant, and 11 that have now been considered synonyms, subspecies, *nomina dubia*, or unrankable. Of the 124 listed as "Critically Endangered (Possibly Extinct)" on the *Red List*, three are known to be extant, six are considered as now extinct, with a further five (Galapagos *Bulimulus* species) undescribed, five synonymized, and five unrankable. And of the 14 listed as extinct in the wild, we considered one to be extant in the wild and five to now be extinct. Thus, excluding undescribed species and species still listed as valid on the *Red List* but that have been synonymized, reduced to subspecies, considered unrankable, or are now thought to be extant, the current *Red List* (IUCN, 2016), in our view correctly lists 386 valid species in the combined categories of Extinct, Critically Endangered (Possibly Extinct), and Extinct in the Wild, which is 44 species fewer than the 430 actually listed by IUCN (Table 2).

The additional information derived from the literature search and expert consultation allowed us to estimate that in fact 638 species are extinct, 380 possibly extinct (EX?), and 14 extinct in the wild, a total of 1,032 species in the combined categories (Appendix Tables A3–5).

Table 2. Numbers of mollusk species considered extinct (EX), critically endangered (possibly extinct) (CR(PE)), and extinct in the wild (EW) in the *Red List* (IUCN, 2016), with species on the *Red List* re-assessed herein, and the results of the present study based on additional literature search and expert consultation.

IUCN category	*Red List*[1]	*Red List* re-assessed	This study[2]
EX	297	268	646
CR(PE) / EX?[3]	119	107	373
EW	14	11	14
Total	**430**	**386**	**1,032**

[1]Includes 11 fossil/subfossil species listed as extinct
[2]Includes 46 fossil/subfossil species listed as extinct
[3]CR(PE) in the *Red List*, EX? in this study

Of these, 47 are known only as "fossil" or "subfossil" but in many of these cases it was not possible to say when they went extinct, perhaps in some cases from natural causes such as non-anthropogenic climate change. For comparability with the approach officially taken by IUCN of focusing on species that have gone extinct since around the year 1500 (though 11 fossil/subfossil species are included in the *Red List*), we might conservatively exclude the 47 fossil/subfossil species in our list and then would consider 591 species as extinct, 380 as possibly extinct, and 14 as extinct in the wild, total 985 species. Even so, our numbers of extinct and possibly extinct species both greatly exceed those of the *Red List*, by more than two and three times respectively. This total is also approximately double the number listed by Régnier et al. (2009).

Of the 1,032 species (Appendix Tables A3–5), 803 are land snails, from 52 families but dominated by species of four Pacific island families, the Amastridae (307 species), which is a Hawaiian endemic family (see below), Endodontidae (92 species), Partulidae (52 species) and Achatinellidae (44 species), as well as one more widespread family (though with greatest diversity in the Pacific), the Charopidae (54 species). Freshwater snails are represented by 177 species from 22 families, with all but two families (Hydrobiidae, 61 species; Pleuroceridae, 32 species) represented by 12 or fewer species. Freshwater bivalves are represented by 46 species from five families, with only the Unionidae (40 species) having more than one or two species. Six marine gastropods are listed.

Régnier et al. (2015)

Régnier et al. (2009) and the updated assessment provided above, have only dealt with species already assessed by IUCN and those additional species that were known to be extinct, possibly extinct, or extinct in the wild, both documented in the literature and as known to biologists with expert knowledge. These species were therefore not a random sample. A more realistic estimate of the true number of mollusk extinctions would only be provided by assessing a random sample of mollusk species.

Therefore, Régnier et al. (2015a), focusing on land snails, generated a rigorously random sample of 200 species from a wide representation of localities across the globe. They evaluated these species based on the IUCN categories and criteria (IUCN, 2012) by reviewing the literature as well as major museum collections. For comparison with this IUCN-based evaluation, they also sent the list of 200 species to numerous land snail experts, asking them to evaluate whether those species for which they had personal knowledge and experience were extinct. For species for which no expert was available, Régnier et al. (2015a) made their own assessment based on collection records. In addition, Régnier et al. (2015a) developed a mathematical probabilistic model, based on collection dates as documented in major museum malacological collections. This model evaluated the probability of extinction for each of the 200 species, and thereby offered an independent means of corroboration (or not) of the expert evaluation.

Based on the IUCN categories and criteria, Régnier et al. (2015a) were only able to evaluate 31 of the 200 species, the other 169 being categorized as Data Deficient. Of the 31, three (1.5% of the 200, but 10% of the evaluated 31) were evaluated as extinct. Under the assumptions that the 200 land snail species in the random sample are representative of the described non-marine molluscan diversity—roughly 30,000 species (Rosenberg, 2014)—and that marine molluscan extinction is negligible compared to non-marine extinction (e.g. Carlton, 1993; but see Peters et al., 2013), extrapolation leads to an estimate of 3,000 extinct mollusk species.

In contrast, the experts were able to evaluate 118 of the 200, the remaining 82 being "Impossible to Assess". Twenty (10% of the 200, but 17% of the evaluated 118) were evaluated as extinct. Note that Régnier et al. (2015a) used slightly different terminology from the IUCN categories in order to draw attention to the differences between the two approaches. The probabilistic model broadly corroborated the expert evaluations in terms of the proportion of species considered extinct.

Of the 76,000 described mollusk species (Rosenberg, 2014), about 46,000 are marine (WoRMS, 2017) and roughly 30,000 non-marine. Therefore, as 10–17% of the 200 land snail species were considered extinct, extrapolation suggests that in fact around 3,000–5,100 mollusk species are extinct, far more than the 297 on the *Red List* (IUCN, 2016), the 532 estimated by Régnier et al. (2009), the 1,032 estimated above updating Régnier et al. (2009), but in the same region as the 3,000 extrapolated from the assessments of Régnier et al. (2015a) based on the IUCN categories and criteria. This estimate of 3,000–5,100 mollusk extinctions, even taking into account that it is based on a small sample, is shocking. And many are going extinct before they have been discovered and described (e.g., Richling and Bouchet, 2013; Sartori et al., 2013; 2014).

WHY ARE NON-MARINE MOLLUSKS GOING EXTINCT?

There are at least four possible causes of non-marine mollusk extinction, which are, for the most part, the same causes of the extinction of non-marine species in general: habitat destruction, impacts of introduced species, exploitation and collecting, and, potentially, climate change.

Habitat Destruction

Urbanization, deforestation, agricultural expansion and exploitation of natural resources have all had impacts on mollusks. Three examples serve to illustrate some of these threats.

Gambier Island Land Snails: Based on collections made by the Bishop Museum (Honolulu) Mangarevan Expedition in 1934 and by the Muséum national d'Histoire naturelle (Paris) in 1997, 46 endemic species have been recorded from the Gambier Islands in the families Euconulidae, Endodontidae, Assimineidae, and Helicinidae (Abdou and Bouchet, 2000; Bouchet and Abdou, 2001; 2003; Richling and Bouchet, 2013). Only three of these species were still extant; the remainder were described from empty shells collected from the shell bank of the soil.

The cause of the extinction of almost this entire fauna was deforestation (Richling and Bouchet, 2013). Deforestation began with the first arrival of Polynesian settlers around 1,000 years ago and reached a peak in the 17th and 18th centuries with the total destruction of the native flora (Conte and Kirch, 2008), no doubt exacerbated after the arrival of Europeans in the early 19th Century. A few of the snail species were still extant in the 1840s–1860s, but no living specimens of all but the three known to be extant have been collected since the 19th Century (Richling and Bouchet, 2013). Similar scenarios have played out across the islands of the Pacific.

***Melanopsis parreyssii* in Romania:** This freshwater species was listed as Critically Endangered on the *Red List* in 2013 (Fehér, 2013). It was deemed Extinct in the Wild in 2016 (Sîrbu and Benedek, 2016). It was extremely narrowly endemic in Romania but had also been introduced to Hungary and Bulgaria. However, by 2010 these introduced populations had vanished (Fehér, 2013; Sîrbu et al., 2013). The Romanian locality was part of a system sustained by a geothermal aquifer that was declared a nature reserve and a Natura 2000 Site of Community Importance. There were lakes and creeks fed by thermal springs, forming the only habitat of *Melanopsis parreyssii*. However, rapidly increasing recent development of the geothermal waters, especially for tourism, led to the springs becoming clogged and the natural thermal lakes diminished, up to the point where the only natural, but shrinking, lake that remained was Peţea (referred to as Băile Episcopiei by Fehér, 2013). By 2011 the spring serving Peţea Lake ceased activity and by 2015 the lake had become little more than a puddle supporting no mollusks except an invasive bivalve (Sîrbu et al., 2013; Sîrbu and Benedek, 2016). Captive breeding efforts have met with little success (Sîrbu and Benedek, 2016). Human greed and disregard for the environment, including laws supposedly protecting it, had led to the destruction of the habitat of this narrowly endemic species and thus its extinction.

***Powelliphanta augusta* in New Zealand:** *Powelliphanta* species are large predatory, worm-eating land snails endemic to New Zealand and most have very small ranges, making them highly vulnerable to habitat destruction (Walker et al., 2008; Boyer et al., 2013). A species of *Powelliphanta*, first collected in 1996 but not recognized as a possible new species until 2003, and confirmed as such by Trewick (2005), was discovered on Mount Augustus, a peak on the Stockton Plateau in New Zealand's South Island and the site of a large open cast coal mine (Trewick et al., 2008). By 2003, much of the snails' habitat had been destroyed, with the entire remaining 8.5 ha of ridge-top habitat under severe threat from the mining. With this imminent threat, and following legal action (see Walker et al., 2008; Boyer et al., 2013), all snails and eggs that could be found were collected and brought into captivity, beginning in 2006. Soon thereafter, all but a tiny piece of snail habitat was destroyed (Walker et al., 2008). Many of the snails were transferred back to the wild at three sites with supposedly similar habitat, but the mortality rate in these populations was such that they were unlikely to survive (Morris, 2010). One of these sites was created by transferring entire habitat from the original site to an area not slated to be mined, but the large trees did not survive well and the habitat was invaded by weedy species (Morris, 2010). The captive snails exhibit slower growth and higher hatchling mortality than estimated in the original wild population (James et al., 2013). Furthermore, a large proportion of the captive snails died following an electrical malfunction in their temperature-controlled facility (James et al., 2013). The species was described as *Powelliphanta augusta* in 2008 (Walker et al., 2008). Although *P. augusta* is not yet extinct, the destruction of its entire habitat by coal mining has left it on the brink.

Impacts of Introduced Species

It is generally difficult to demonstrate definitively that an invasive species has caused the extinction of another species. For example, following the zebra mussel (*Dreissena polymorpha*) invasion of North America beginning around 1985, many of the native freshwater mussels (Unionoida) were thought to be doomed (Ricciardi et al., 1998). At localities with high densities of *D. polymorpha*, local populations of native mussels were being extirpated and some of the native species were in steep decline or becoming regionally extinct. Over 60 species were thought to be in danger of global extinction from the combined effects of zebra mussels and habitat degredation (Ricciardi et al., 1998). However,

a decade later, Strayer and Malcom (2007), focusing on four species in the Hudson River, showed that although they had declined steeply following zebra mussel invasion, by 2000–2004 populations of these species had stabilized at 4–22% of their pre-invasion densities, offering a slender hope that the native mussels might be able to co-exist with the invaders, albeit at much lower densities (Strayer and Malcom, 2007).

In contrast, the prime example of an invasive species causing extinction of mollusk species is the introduction of the predatory snail *Euglandina rosea* to the islands of the Pacific, notably to the Hawaiian Islands and the Society Islands of French Polynesia but also elsewhere (e.g., Cowie and Cook, 2001), in poorly considered efforts to control the invasive giant African snail, *Achatina fulica* (Hadfield, 1986; Murray et al., 1988). The clearest evidence of a direct impact was that as *E. rosea* spread across the island of Moorea, the endemic *Partula* tree snail species vanished in its wake; it did not control *A. fulica* (Murray et al., 1988; Cowie, 2001). On the other islands of the Society group the same story played out (Coote and Loève, 2003; Gerlach, 2016).

In Hawaii, the combination of *E. rosea* and invasive rats, following on from habitat destruction, has caused the decline of endemic achatinelline tree snails (Hadfield et al., 1993), and another introduced predatory snail, *Oxychilus alliarius*, may yet impact endemic Hawaiian species, notably the single species in the endemic monotypic helicarionid genus *Kaala* (Curry et al., 2016). The invasive predatory flatworm *Platydemus manokwari* has caused the extinction of endemic Pacific island snails, notably in the Ogasawara Islands (Chiba and Cowie, 2016). Competition between invasive and native snails may also be important, but no definitive instances of this have been documented (Cowie, 2005).

The impacts of invasive species are often inextricably linked to those of habitat destruction or modification, as invasive species, such as rats (e.g., Athens, 2009), may drastically alter habitat, and habitat alteration may facilitate the spread of invasive species (Didham et al., 2007). As such, they can be at least the partial cause of extinction. However, invasive species may act in concert with or consecutively with habitat alteration, making it difficult, with some clear exceptions, to say that invasive species, per se, have been the cause of specific mollusk species extinctions.

Exploitation and Collecting

Numerous non-marine mollusk species are exploited for human consumption. In Europe, and especially in countries bordering the Mediterranean, various of the larger species of land snails are collected and eaten, most notably *Helix pomatia*, the "escargot de Bourgogne", and *Cornu aspersum*, the "petit gris", both of which are readily available in most French markets, but also more widely. However, although *C. aspersum* remains abundant and widespread in western Europe, *H. pomatia* has declined, notably in France, and efforts are increasingly being made to culture it for export, especially in eastern Europe (Ligaszewski et al., 2007). Nonetheless, *H. pomatia* is listed as of Least Concern on the *Red List* (IUCN, 2016). Various other species are eaten around the Mediterranean (Yildirim et al., 2004) but none seems to have attracted conservation concern. The collection in the wild for the restaurant trade, in combination with habitat loss and alien species, has endangered the endemic "bulimes" (genus *Placostylus*) of New Caledonia (Brescia et al., 2008; Neubert et al., 2009). In Asia, various species of Ampullariidae, Viviparidae, and Pachychilidae in particular are eaten, as are a number of clams and mussels (e.g., Köhler et al., 2012), and Achatinidae are eaten in West Africa (e.g., Nyoagbe et al., 2016); but none of these species has attracted great concern because of this.

There are a few records of land snails being used for medicinal purposes, e.g., *Theba pisana* (Benítez, 2011) and *Achatina fulica* (Cowie and D.G. Robinson, 2003), and religious purposes, e.g., *Achatina fulica* (Neto et al., 2012), and they may be a significant part of local rural economies (Osemeobo, 1991); they may also be introduced beyond their native range for such religious purposes (Vázquez et al., 2016). But there is no evidence that these usages have led to the decline and certainly not extinction of these species.

In the 19th Century, freshwater mussels (Unionida) were commercially harvested for their pearls, notably in the United States; over-harvesting led to decline of the populations and the fishery was largely abandoned (Neves, 1999; Anthony and Downing, 2001). However, soon thereafter, the demand for shells of freshwater mussels for the button industry burgeoned, causing further declines and adding to the already serious and increasing threats from habitat degredation; but this industry essentially died out with the advent of plastics (Neves, 1999; Anthony and Downing, 2001; Strayer et al., 2004), although it persists in other parts of the world (Beasley, 2001). However, the discovery in Japan that mussel shell material could act as nuclei for the production of cultured pearls, resulted in a further phase of exploitation of mussels in the United States for export, although demand declined drastically by the late 1990s (Neves, 1999) Although habitat degredation has been generally considered the primary cause of mussel decline, over-exploitation has also been important (Strayer et al., 2004).

The hobby of shell-collecting is generally more focused on marine than on non-marine species, with some marine taxa, for instance in the genus *Conus*, threatened as a result (Peters et al., 2013). Nonetheless, among non-marine species there are a few notable instances in which shell collecting and ornamental use may have been at least in part responsible for the decline and perhaps extinction of certain species (Cowie, 2004). Most notably, collecting of snails by late 19th and early 20th Century shell collectors quite possibly had an important impact on some of the larger and more colorful Hawaiian species, primarily but by no means exclusively the beautifully colored and patterned Achatinellinae

(Hadfield, 1986). Compared to marine species, there is a much more limited collectors' trade in shells of non-marine species, which nonetheless may lead to endangerment. However, the legal instruments of control (notably the Convention on International Trade in Endangered Species (CITES)) list only three non-marine gastropod genera: the genus *Achatinella*, with 39 species listed as Extinct or Critically Endangered by IUCN (2016), the genus *Polymita*, with no species listed, and *Papustyla pulcherrima*, the Manus Island (off the north coast of New Guinea) green tree snail, which is listed as Near Threatened by IUCN (2016) (see also Whitmore, 2016). The collection of the 10,000 or so shells of the partulid tree snail *Eua zebrina* that once made up the chandeliers in the lobby of American Samoa's then main hotel surely must have significantly reduced at least some populations of that species (Cowie, 1993).

Overall, therefore, exploitation and collecting have not been a major cause of mollusk extinction, with a number of notable exceptions.

Climate Change

Gerlach (2007) declared that *Rhachistia aldabrae*, an endemic cerastid from Aldabra Atoll that was still locally abundant in the 1970s (Gerlach, 2009), had gone extinct in the late 1990s as a result of declining rainfall. It was therefore placed on the *Red List* as Extinct (Gerlach, 2009). This is the only instance of a mollusk being reported as having gone extinct as a result of climate change. However, in 2014 it was discovered alive (Battarbee, 2014). Nonetheless, there is only one tiny population (J. Gerlach, pers. comm.) and it seems likely that with ongoing climate change it may yet succumb. The *Red List* (IUCN, 2016) has not yet been updated.

Baur and Baur (1993) concluded that the local extirpation of the widespread European land snail *Arianta arbustorum* at sites around the city of Basel, Switzerland, had resulted from climate warming in otherwise suitable areas close to extensive urban development, and that sites from which *A. arbustorum* had disappeared had higher surface temperatures than sites where it remained. The same authors (Baur and Baur, 2013) compared historical records from 1916–1917 with survey results from 2011–2012 on nine mountain slopes in Switzerland. They found that the upper elevational limit for *A. arbustorum* had risen 164 m in the 95 year period, during which mean annual temperature in the area had risen 1.6 °C. Although only a local impact, this study demonstrated the potential for climate change to affect populations of land snails.

Similarly, Pearce and Paustian (2013) undertook extensive elevational surveys in Pennsylvania, USA, to assess whether, with climate warming, species forced ever upward would eventually have nowhere further to retreat to (cf. similar studies on arthropods: Meyer et al., 2015). Of the 69 species recorded, five appeared especially susceptible. This kind of susceptibility is of particular concern on oceanic islands, especially in the Pacific. On many Pacific islands, habitat destruction and the introduction of invasive species at lower elevations has resulted in most of the remaining endemic land snail species being confined to higher elevation refugia (Durkan et al., 2013), either because their lower elevation populations have been extirpated or because they are evolutionarily adapted to the lower temperatures at these higher elevations and historically only ever occurred there. As such, with limited opportunity to move to higher elevations as the climate warms, they face extinction.

Thus, there is no evidence that climate change has caused the extinction of any non-marine mollusk species. However, continued warming will probably have more serious effects in the future, and ocean acidification resulting from raised carbon dioxide levels may impact marine species (Peters et al., 2015).

EXTINCTION ON PACIFIC ISLANDS: A CASE STUDY

Among the species assessed as extinct by Régnier et al. (2009), more than 70% were from oceanic islands and most of these were from the Hawaiian Islands, French Polynesia and the Mascarene Islands. Previous authors have suggested that 65–90% of the Hawaiian land snail species have gone extinct (Solem, 1990; Cowie and A.C. Robinson, 2003; Lydeard et al., 2004). The proportion differs among families, but three groups (Achatinellinae, Amastridae, Endodontidae) appear to have suffered "catastrophic extinction" (Solem, 1990; and see above).

To begin to get a more accurate assessment of the level of extinction in Hawaiian land snails, Régnier et al. (2015b) focused on the Amastridae, a family endemic to the Hawaiian Islands and with 325 known valid species (Cowie et al., 1995). Rather than using the rigid IUCN categories and criteria (IUCN, 2012), they took a less rigorous approach similar to that taken by Régnier et al. (2015a). They based their assessments on a comparison of information from historical collections and archived field notes in the Bishop Museum, with data from modern extensive surveys undertaken throughout the Hawaiian Islands by K.A. Hayes, N.W. Yeung, and collaborators between 2004 and 2013. They also consulted a diversity of experts with experience in the Hawaiian land snail fauna. A species was considered extinct if it had not been found since 2004 at any recently surveyed location where it had formerly been recorded. In addition, and again taking a similar approach to that adopted by Régnier et al. (2015a) in order to provide independent corroboration, Régnier et al. (2015b) undertook a statistical assessment of extinction probabilities, based on collection years and using the methods of Thompson et al. (2013) and Lee (2014).

Of the 325 species, 131 were assessed as extinct; there was insufficient evidence of extinction for 179, although most of these can probably be considered extinct (and were considered possibly extinct in the updated analysis

of global extinctions, above); but only 15 were considered definitively extant (three subsequently found extant; N.W. Yeung and K.A. Hayes, pers. comm.). Thus, a minimum of 131 (40%) and maximum 310 (95%) were considered extinct. The probabilistic assessment was consistent with the expert assessment: the probabilities of being extant for those species assessed as extinct was <0.01 (111 species), <0.1 (16 species) and 0.1–0.3 (4 species); and for those species assessed as extant it was 0.38–0.93 (15 species); the species for which there was insufficient evidence of extinction were not assessed probabilistically. The *Red List* (IUCN, 2016) lists only 33 amastrid species (10%) as extinct.

There have been five phases of amastrid extinction, discussed in more detail by Régnier et al. (2015b), as follows.

1) Description as fossils or subfossils and not known to be extant, but it is not possible currently to determine when they went extinct, i.e., prior to or after human colonization of the Hawaiian Islands, or prior to or after around the year 1500.
2) Subsequent to the first colonization of the islands by Polynesians, 800–1000 years ago, which led to considerable habitat destruction and introduction of a number of alien species.
3) Following European colonization, when extensive additional habitat destruction took place and highly destructive invasive alien species were introduced.
4) Following the advent of large-scale agriculture at the end of the 19th Century, at the time of a major increase in land snail extinction rate globally, identified as around 1895 by Régnier et al. (2015a).
5) After 1945 and the end of the Second World War, with the increased military activity, tourism, commerce, urbanization and rapidly increasing introduction of invasive species, including snails (Cowie, 1998).

If the extinction rate were constant over this roughly 1,000 year period, it would have been between roughly 0.4 and 1.0% of the fauna per decade, given the extremes of 131 and 310 of the 325 amastrid species having gone extinct. However the rate was certainly not constant but probably has increased in a roughly exponential and step-wise manner over time. Régnier et al. (2015b) therefore modeled a number of scenarios reflecting this increasing rate. The overall rates obtained ranged from 0.4% of the amastrid fauna per decade (131 species extinct, beginning in the year 1000, as above) to 14% per decade (310 species extinct, beginning in 1945). These scenarios are certainly over-simplistic, but nonetheless provide a framework for discussion.

DISCUSSION

The most conservative estimate of 0.4% per decade for the Hawaiian amastrid extinction rate is similar to the global biodiversity extinction rate of < 1% per decade estimated by Costello et al. (2013). However, this extinction rate is probably not reflective of the true rate of amastrid extinction, as not only is it based on a very conservative estimate of the number of species that have gone extinct (131) but it assumes a constant rate since the year 1000. Undoubtedly, the rate has increased over the millenium and Régnier et al. (2015b) suggested that a rate of around 5% per decade over the last 150–200 years would be more realistic, indeed still rather conservative, given the maximum rate they estimated of 14% per decade. A rate of 5% would lead to a loss of > 50% of a fauna within 150 years (Costello et al., 2013). Indeed, for the amastrids, with only 18 of 325 species known to be extant (i.e., including the three species discovered alive since Régnier et al., 2015b; see above), this scenario seems to have already played itself out.

This rate (5% per decade) is much higher than the global estimate of the loss over the last 500 years or so of 3,000–5,100 (10–17%) of the 30,000 known land snail species, as estimated by Régnier et al. (2015a) and outlined above. The amastrids, however, may be an extreme case, although land snail groups from other Pacific islands have suffered similar fates, notably the Endodontidae (Solem, 1976; Zimmerman et al., 2009; Sartori et al., 2013; 2014) and Partulidae (Coote et al., 2003; Gerlach, 2016), and many extinct species continue to be found, as empty shells, even before their scientific description (e.g., Richling and Bouchet, 2013). Oceanic island biotas are in general much more susceptible to extinction than more buffered continental faunas (Triantis et al., 2010). And some taxa may be more susceptible than others. Therefore it may be dangerous to base generalizations regarding extinction rates on global estimates, though even these, such as the loss of 10–17% of land snail species in 500 years described here, are cause for great concern. While it is crucial to increase awareness of the high level of global extinction, subsuming more local extinction rates, especially of particularly susceptible faunas such as those of oceanic islands, or of particularly susceptible taxa such as the Amastridae, under global rates will doom those plants and animals to extinction as their special vulnerability and need for conservation will be overlooked, or at least not adequately appreciated.

If we assume that 1) the 200 land snail species sampled by Régnier et al. (2015a) are representative of known non-marine invertebrate diversity and their extinction rate, 2) three-quarters of species are non-marine (Mora et al., 2011), and 3) marine extinctions are negligible compared with non-marine extinctions (only four marine mollusks are considered as extinct; IUCN (2016), and see above), then approximately 7.5–13% of all species have gone extinct since around 1500. This is orders of magnitude greater than the 860 (0.05% of 2 million) listed as extinct by IUCN (2016). The biodiversity crisis is real.

But what of the IUCN? The studies reviewed herein have shown that it is inappropriate to use the IUCN *Red List* as a source of data on global extinction rates (except for mammals and birds), and more generally that

assessing overall levels of threat to all biodiversity based on the species listed by IUCN seriously downplays that threat, notably because the great majority of biodiversity (invertebrates) has not been evaluated. A similar critique was voiced by Possingham et al. (2002), who argued that threatened species lists (such as the IUCN *Red List*) should not be used to indicate the overall status of biodiversity and changes in it, largely because of uneven taxonomic treatment and variation in observational effort (as described above for vertebrates compared to invertebrates). Nonetheless, IUCN is the premier and most influential global conservation organization. But its goal is to "highlight taxa threatened with extinction, and thereby promote their conservation" (IUCN, 2016); documenting extinction is incidental to this goal as once extinct a species cannot be conserved. For terrestrial vertebrates IUCN is well on the way to achieving its goal, but invertebrates present a daunting challenge both because of their immense diversity and because of the lack of adequate data to apply the IUCN criteria for the vast majority of them.

Major focused efforts by IUCN continue to be made to evaluate additional mollusk species (e.g., Seddon, 2011; 2014; 2015; Pippard, 2012; Peters et al., 2013; Seddon et al., 2014; Allen et al., 2016; Böhm and Allcock, 2016; Neubert et al., 2017). These efforts have focused on particular taxa, habitats and geographic locations that were deemed *a priori* as especially in need of attention, i.e., to address the IUCN goals of highlighting taxa in need of conservation (above), and for which funding could be obtained. Nonetheless, at the current rate it will be many years before all mollusks, or even all non-marine mollusks, have been assessed. The approach we have taken in the two studies reviewed herein (Régnier et al., 2015a, b), as well as our update of the analysis of Régnier et al. (2009) based on new information, is an attempt to speed up the evaluation process and to develop a method that allows global trends to be more realistically determined. Admittedly, our approach is less rigorous than the process of applying the IUCN criteria to assign species to the IUCN categories, with peer review required (when at best only one specialist has any knowledge of the fauna), but is considerably quicker and more cost-effective. While there is a chance that our approach might incorrectly list some species as extinct and thereby cut them off from conservation attention, it has the potential to identify many more species in need of conservation, species that would be listed as Data Deficient by IUCN and therefore also ignored. Our approach also has the advantage that it can provide a much more realistic overview of the biodiversity crisis than can the *Red List*, especially regarding the extraordinary levels of extinction, which was our immediate focus in the studies reviewed above. Nonetheless, IUCN remains the preeminent global conservation agency with a crucial role in identifying conservation needs and developing global conservation strategies. Our efforts do not in any way compromise those roles.

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APPENDIX

Table A1. Species considered extinct, extinct in the wild or critically endangered (possibly extinct) by Régnier et al. (2009) and/or the *Red List* (IUCN, 2016) but now known or thought to be extant (or unrankable). DD – data deficient, VU – vulnerable, EN – endangered, CR – critically endangered, EW – extinct in the wild, EX – Extinct.

Species	*Red List*	Régnier et al.	References indicating species is extant
ACHATINELLIDAE			
Achatinella livida Swainson, 1828	EX	Extant	M.G. Hadfield, pers. comm.
Auriculella uniplicata (Pease, 1868)	EX	Extant	N.Y. Yeung, pers. comm.
Perdicella fulgurans Sykes, 1900	EX	Extant	M.G. Hadfield, pers. comm.
Perdicella maniensis (Pfeiffer, 1856)	EX	Extant	M.G. Hadfield, pers. comm.
Perdicella zebrina (Pfeiffer, 1856)	EX	Extant	M.G. Hadfield, pers. comm.
CERASTIDAE			
Rhachistia aldabrae (Martens, 1898)	EX	EX	Battarbee, 2014
CYCLOPHORIDAE			
Cyclophorus horridulum (Morelet, 1882)	EX	EX?	Abdou et al., 2004
Cyclosurus mariei Morelet, 1881	EX	–	Abdou et al., 2004
HYDROBIIDAE			
Belgrandiella zermanica Radoman, 1973	VU	EX	Slapnik and Lajtner, 2011
Bracenica spiridoni Radoman, 1973	EN	EX	Pešić, 2010a; Pešić and Glöer, 2013
Islamia zermanica Radoman, 1973	CR(PE)	EX	Beran et al., 2016
Marstonia castor (Thompson, 1977)	CR	EX?	Johnson et al., 2013
Mercuria globulina (Letourneux and Bourguignat, 1887)	EX	–	Glöer et al., 2015
Tanousia zrmanjae (Brusina, 1866)	CR	EX	Beran, 2011; Falniowski, 2011a
Vinodolia fiumana Radoman, 1973	EN	EX	Szarowska et al., 2013; Falniowski and Seddon, 2014
Vinodolia fluviatilis (Radoman, 1973)	EN	EX	Beran, 2011; Falniowski, 2011b
Vinodolia gluhodolica (Radoman, 1973)	EN	EX	Pešić, 2010b; Glöer and Pešić, 2014
LITHOGLYPHIDAE			
Clappia cahabensis Clench, 1965	EX	–	Johnson et al., 2013
Somatogyrus alcoviensis Krieger, 1915	EX	–	Johnson et al., 2013
Somatogyrus amnicoloides Walker, 1915	EX	EX	"unrankable", Johnson et al., 2013
Somatogyrus crassus Walker, 1904	CR(PE)	–	"unrankable", Johnson et al., 2013
Somatogyrus currierianus Lea, 1863	CR(PE)	–	"unrankable", Johnson et al., 2013
Somatogyrus hendersoni Walker, 1909	CR(PE)	–	"unrankable", Johnson et al., 2013
Somatogyrus humerosus Walker, 1906	CR(PE)	–	"unrankable", Johnson et al., 2013
Somatogyrus nanus Walker, 1904	CR(PE)	–	"unrankable", Johnson et al., 2013
LITTORINIDAE			
Littoraria flammea (Philippi, 1847)	EX	EX	Dong et al., 2015
NEOCYCLOTIDAE			
Incerticyclus martinicensis (Shuttleworth, 1857)	EX	EX	Delannoye et al., 2015
PARTULIDAE			
Partula leefei Smith, 1897	–	EX	Gerlach, 2016
Partula nodosa Pfeiffer, 1853	EW	EW	Gerlach, 2016
Samoana annectens (Pease, 1864)	DD	EX	Gerlach, 2016
Samoana diaphana (Crampton and Cooke, 1953)	EN	EX	Gerlach, 2016
Samoana inflata (Reeve, 1842)	EX	–	Gerlach, 2016
PHYSIDAE			
Physella columbiana Keep, 1887	–	EX?	Johnson et al., 2013
Physella hemphilli Taylor, 2003	–	EX?	Johnson et al., 2013
PLANORBIDAE			
Rhodacmea filosa (Conrad, 1834)	CR	EX	Ó Foighil et al., 2011
PLEUROCERIDAE			
Elimia lachryma (Reeve, 1861)	EX	–	Johnson et al., 2013
Elimia melanoides (Conrad, 1834)	–	EX	Minton et al., 2003; Johnson et al., 2013
Elimia mutabilis (Lea, 1862)	–	EX?	Johnson et al., 2013
Elimia troostiana (Lea, 1838)	CR(PE)	–	Johnson et al., 2013
Elimia varians (Lea, 1861)	VU	EX	Cordeiro and Perez, 2012
Elimia vanuxemiana Lea, 1843	EX	–	Johnson et al., 2013
Leptoxis compacta (Anthony, 1854)	EX	EX	Whelan et al., 2012

(*Continued*)

Table A1. (cont.)

Species	*Red List*	Régnier et al.	References indicating species is extant
Leptoxis foremanii (Lea, 1843)	EX	EX	Johnson et al., 2013
STREPTAXIDAE			
Gulella mayottensis (Connolly, 1885)	EX	–	Abdou et al., 2004
VIVIPARIDAE			
Tchangmargarya yangtsunghaiensis (Tchang and Tsi, 1949)	CR(PE)	–	Zhang et al., 2015
UNIONIDAE			
Pleurobema taitianum (Lea, 1834)	EN	EX	Cummings and Cordeiro, 2012

Table A2. Species listed on the *Red List* (IUCN, 2016) or by Régnier et al. (2009) as extinct or critically endangered (possibly extinct) but now considered as subspecies or synonyms of other species, as *nomina dubia*, or that are undescribed. These are excluded from the present analysis.

Species	*Red List*	Régnier et al.	Source for subspecies/synonym/ undescribed status
HYDROBIIDAE			
Bythiospeum dubium (Geyer, 1904)	CR(PE)	–	Synonym of *Bythiospeum acicula*; Richling et al., 2016
Bythiospeum gonostoma (Geyer, 1905)	CR(PE)	–	Synonym of *Bythiospeum acicula*; Richling et al., 2016
Bythiospeum putei (Geyer, 1904)	CR(PE)	–	Synonym of *Bythiospeum acicula*; Richling et al., 2016
Bythiospeum turritum (Clessin, 1877)	CR(PE)	–	Synonym of *Bythiospeum acicula*; Richling et al., 2016
Pseudamnicola desertorum (Bourguignat, 1862)	EX 2010	–	Synonym of *Pseudamnicola letourneuxiana*; Glöer et al., 2010
ORTHALICIDAE			
Bulimulus sp. nov. '*josevillani*'	CR(PE)		undescribed; IUCN (2016)
Bulimulus sp. nov. '*krameri*'	CR(PE)		undescribed; IUCN (2016)
Bulimulus sp. nov. '*nilsodlmeri*'	CR(PE)		undescribed; IUCN (2016)
Bulimulus sp. nov. '*tuideroyi*'	CR(PE)		undescribed; IUCN (2016)
Bulimulus sp. nov. '*vanmoli*'	CR(PE)		undescribed; IUCN (2016)
PARTULIDAE			
Partula callifera Pfeiffer, 1857	EX		Subspecies of *Partula dentifera*; Gerlach, 2016
Partula candida Crampton, 1956	EX		Subspecies of *Partula dentifera*; Gerlach, 2016
Partula cedista Crampton, 1956	EX		Subspecies of *Partula dentifera*; Gerlach, 2016
Partula citrina Pease, 1866	EX		Subspecies of *Partula dentifera*; Gerlach, 2016
Partula formosa Garrett, 1884	EX		Subspecies of *Partula dentifera*; Gerlach, 2016
Partula imperforata Pfeiffer, 1877	EX		Subspecies of *Partula dentifera*; Gerlach, 2016
Partula raiatensis Garrett, 1884	EX		Synonym of *Partula imperforata*; Gerlach, 2016
PLEUROCERIDAE			
Elimia timida timida Goodrich, 1942	–	EX	Dillon and Robinson, 2011
UNIONIDAE			
Nodularia cariei (Germain, 1919)	EX 1996	EX	Synonym of *Coelatura aegyptiaca*; Graf and Cummings, 2009
Unio madagascariensis Sganzin, 1842	EX 2016	–	*Nomen dubium*; Graf and Cummings, 2009
Unio malgachensis Germain, 1911	EX 2016	–	*Nomen dubium*; Graf and Cummings, 2009

Table A3. Terrestrial species considered extinct (EX), possibly extinct (EX?) or extinct in the wild (EW) in the present study, compared with their status as evaluated by Régnier et al. (2009), and on the *Red List* (IUCN, 2016). *Red List* categories are extinct (EX), extinct in the wild (EW), critically endangered (possibly extinct) (CR(PE)), critically endangered (CR), and data deficient (DD); the date of the IUCN evaluation follows the status. EX? is treated as equivalent to CR(PE). A dash indicates the species was not evaluated. Sources are only provided if the status in this study differs from the later of IUCN (2016) and Régnier et al. (2009). Species explicitly described as fossil or subfossil are asterisked.

Species	Red List	Régnier et al., 2009	This study	Source for revised status; comments
ACHATINELLIDAE				
Achatinella abbreviata Reeve, 1850	EX 1996	EX	EX	
Achatinella apexfulva (Dixon, 1789)	–	–	EX?	B.S. Holland, pers. comm., 2016
Achatinella buddii Newcomb, 1854	EX 1990	EX	EX	
Achatinella caesia Gulick, 1858	EX 1990	EX	EX	
Achatinella casta Newcomb, 1854	EX 1990	EX	EX	
Achatinella cestus Newcomb, 1854	–	–	EX?	USFWS, 1993
Achatinella decora (Férrusac, 1821)	EX 1990	EX	EX	
Achatinella dimorpha Gulick, 1858	EX 1990	EX	EX	
Achatinella elegans Newcomb, 1854	EX 1996	EX	EX	
Achatinella juddii Baldwin, 1895	EX 1996	EX	EX	
Achatinella juncea Gulick, 1856	EX 1996	EX	EX	
Achatinella lehuiensis Smith, 1873	EX 1990	EX	EX	
Achatinella papyracea Gulick, 1856	EX 1990	EX	EX	
Achatinella phaeozona Gulick, 1856	–	–	EX?	USFWS 1993
Achatinella rosea Swainson, 1828	–	–	EX	USFWS 1993
Achatinella spaldingi Pilsbry and Cooke, 1914	EX 1990	EX	EX	
Achatinella stewartii (Green, 1827)	–	–	EX?	B.S. Holland, pers. comm., 2016
Achatinella thaanumi Pilsbry and Cooke, 1914	EX 1990	EX	EX	
Achatinella valida Pfeiffer, 1855	EX 1990	EX	EX	
Achatinella viridans Mighels, 1845	–	–	EX?	USFWS, 1993
Achatinella vittata Reeve, 1850	–	–	EX	USFWS, 1993
Achatinella vulpina (Férrusac, 1821)	–	–	EX	USFWS, 1993
Auriculella expansa Pease, 1868	EX 1994	EX	EX	
Hotumatua anakenana Kirch et al., 2009	–	–	EX	Kirch et al., 2009
Lamellidea monodonta (Pilsbry and Hirase, 1904)	EX 1994	EX	EX	
Lamellidea nakadai (Pilsbry and Cooke, 1915)*	EX 1994	–	EX	
Newcombia canaliculata (Baldwin, 1893)	–	–	EX	B.S. Holland, pers. comm., 2016
Newcombia gagei Severns, 2009*	–	–	EX	Severns, 2009
Newcombia perkinsi Sykes, 1896	–	–	EX	B.S. Holland, pers. comm., 2016
Newcombia pfeifferi (Newcomb, 1853)	–	–	EX	B.S. Holland, pers. comm., 2016
Newcombia philippiana (Pfeiffer, 1857)	EX 1994	–	EX	
Newcombia sulcata (Pfeiffer, 1857)	–	–	EX	B.S. Holland, pers. comm., 2016
Partulina variabilis (Newcomb, 1854)	–	–	EW	
Partulina confusa (Sykes, 1900)	CR 1996	EX	EX	
Partulina crassa (Newcomb, 1854)	EX 1986	EX	EX	
Partulina dubia (Newcomb, 1853)	–	–	EX	B.S. Holland, pers. comm., 2016
Partulina horneri (Baldwin, 1895)	–	EX	EX	
Partulina montagui Pilsbry, 1913	EX 1986	EX	EX	
Partulina semicarinata (Newcomb, 1854)	–	–	EW	
Perdicella carinella (Baldwin, 1906)	–	–	EX	B.S. Holland, pers. comm., 2016
Perdicella ornata (Newcomb, 1854)	–	–	EX	B.S. Holland, pers. comm., 2016
Perdicella thwingi (Pilsbry and Cooke, 1914)	–	–	EX	B.S. Holland, pers. comm., 2016
Perdicella zebra (Newcomb, 1853)	EX 1994	EX	EX	
Tornelasmias capricorni Iredale, 1944	EX 1996	EX	EX	
AMASTRIDAE				
Amastra abavus Hyatt and Pilsbry, 1911)	–	–	EX?	Régnier et al., 2015
Amastra aemulator Hyatt and Pilsbry, 1911)	–	–	EX?	Régnier et al., 2015
Amastra affinis (Newcomb, 1854)	–	–	EX	Régnier et al., 2015
Amastra albocincta Pilsbry and Cooke, 1914	–	–	EX?	Régnier et al., 2015
Amastra albolabris (Newcomb, 1854)	EX 1994	EX	EX	Régnier et al., 2015
Amastra amicta Smith, 1873	–	–	EX?	Régnier et al., 2015

(*Continued*)

Table A3. (cont.)

Species	Red List	Régnier et al., 2009	This study	Source for revised status; comments
Amastra anthonii (Newcomb, 1861)	–	–	EX	Régnier et al., 2015
Amastra antiqua (Baldwin, 1895)*	–	–	EX	Régnier et al., 2015
Amastra assimilis (Newcomb, 1854)	–	–	EX	Régnier et al., 2015
Amastra aurostoma Baldwin, 1896)	–	–	EX?	Régnier et al., 2015
Amastra badia (Baldwin, 1895)	–	–	EX?	Régnier et al., 2015
Amastra baldwiniana Hyatt and Pilsbry, 1911	–	–	EX	Régnier et al., 2015
Amastra biplicata (Newcomb, 1854)	–	–	EX?	Régnier et al., 2015
Amastra borcherdingi Hyatt and Pilsbry, 1911	–	–	EX?	Régnier et al., 2015
Amastra breviata Baldwin, 1895)	–	–	EX?	Régnier et al., 2015
Amastra caputadamantis Hyatt and Pilsbry, 1911*	–	–	EX	Régnier et al., 2015
Amastra conica Baldwin, 1906*	–	–	EX	Régnier et al., 2015
Amastra conifera Smith, 1873	–	–	EX?	Régnier et al., 2015
Amastra cornea (Newcomb, 1854)	EX 1994	EX	EX	Régnier et al., 2015
Amastra crassilabrum (Newcomb, 1854)	EX 1994	EX	EX	Régnier et al., 2015
Amastra cyclostoma (Baldwin, 1895)	–	–	EX	Régnier et al., 2015
Amastra davisiana Cooke, 1908	–	–	EX	Régnier et al., 2015
Amastra decorticata Gulick, 1873	–	–	EX?	Régnier et al., 2015
Amastra delicata Cooke, 1933	–	–	EX	Régnier et al., 2015
Amastra durandi Ancey, 1897	–	–	EX?	Régnier et al., 2015
Amastra dwightii Cooke, 1933	–	–	EX	Régnier et al., 2015
Amastra elegantula Hyatt and Pilsbry, 1911	–	–	EX?	Régnier et al., 2015
Amastra elephantina Cooke, 1917*	–	–	EX	Régnier et al., 2015
Amastra elliptica Gulick, 1873	–	–	EX?	Régnier et al., 2015
Amastra elongata (Newcomb, 1853)	EX 1996	EX	EX	Régnier et al., 2015
Amastra eos Pilsbry and Cooke, 1914	–	–	EX?	Régnier et al., 2015
Amastra extincta (Pfeiffer, 1856)*	–	–	EX	Régnier et al., 2015
Amastra farcimen (Pfeiffer, 1857)	–	–	EX	Régnier et al., 2015
Amastra flavescens (Newcomb, 1854)	–	–	EX	Régnier et al., 2015
Amastra flemingi Cooke, 1917*	–	–	EX	Régnier et al., 2015
Amastra forbesi Cooke, 1917*	EX 1996	EX	EX	Régnier et al., 2015
Amastra fossilis Baldwin, 1903*	–	–	EX	Régnier et al., 2015
Amastra fragilis Pilsbry and Cooke, 1914	–	–	EX?	Régnier et al., 2015
Amastra fragosa Cooke, 1917	–	–	EX?	Régnier et al., 2015
Amastra fraterna Sykes, 1896	–	–	EX?	Régnier et al., 2015
Amastra globosa Cooke, 1933*	–	–	EX	Régnier et al., 2015
Amastra gouveii Cooke, 1917	–	–	EX?	Régnier et al., 2015
Amastra grayana (Pfeiffer, 1856)	–	–	EX?	Régnier et al., 2015
Amastra gulickiana Hyatt and Pilsbry, 1911	–	–	EX?	Régnier et al., 2015
Amastra hawaiiensis Hyatt and Pilsbry, 1911	–	–	EX?	Régnier et al., 2015
Amastra hitchcocki Cooke, 1917*	–	–	EX	Régnier et al., 2015
Amastra humilis (Newcomb, 1855)	–	–	EX?	Régnier et al., 2015
Amastra hutchinsonii (Pease, 1862)	–	–	EX?	Régnier et al., 2015
Amastra implicata Cooke, 1933	–	–	EX	Régnier et al., 2015
Amastra inflata (Pfeiffer, 1856)	–	–	EX?	Régnier et al., 2015
Amastra inopinata Cooke, 1933*	–	–	EX	Régnier et al., 2015
Amastra irwiniana Cooke, 1908	–	–	EX	Régnier et al., 2015
Amastra johnsoni Hyatt and Pilsbry, 1911	–	–	EX?	Régnier et al., 2015
Amastra juddii Cooke, 1917	–	–	EX	Régnier et al., 2015
Amastra kalamaulensis Pilsbry and Cooke, 1914	–	–	EX?	Régnier et al., 2015
Amastra kauaiensis (Newcomb, 1860)	–	–	EX	Régnier et al., 2015
Amastra kaunakakaiensis Pilsbry and Cooke, 1914	–	–	EX	Régnier et al., 2015
Amastra knudsenii (Baldwin, 1895)	–	–	EX	Régnier et al., 2015
Amastra laeva Baldwin, 1906	–	–	EX	Régnier et al., 2015
Amastra lahainana Pilsbry and Cooke, 1914	–	–	EX	Régnier et al., 2015
Amastra lincolata (Newcomb, 1853)	–	–	EX?	Régnier et al., 2015
Amastra luctuosa (Pfeiffer, 1856)	–	–	EX?	Régnier et al., 2015
Amastra luteola (Férrusac, 1825)	–	–	EX?	Régnier et al., 2015
Amastra magna (Adams, 1851)	–	–	EX?	Régnier et al., 2015

(*Continued*)

Table A3. (cont.)

Species	Red List	Régnier et al., 2009	This study	Source for revised status; comments
Amastra makawaoensis Hyatt and Pilsbry, 1911	–	–	EX	Régnier et al., 2015
Amastra malleata Smith, 1873	–	–	EX?	Régnier et al., 2015
Amastra mastersi (Newcomb, 1854)	–	–	EX?	Régnier et al., 2015
Amastra melanosis (Newcomb, 1854)	–	–	EX	Régnier et al., 2015
Amastra metamorpha Pilsbry and Cooke, 1914	–	–	EX	Régnier et al., 2015
Amastra mirabilis Cooke, 1917	–	–	EX	Régnier et al., 2015
Amastra modesta (Adams, 1851)	–	–	EX?	Régnier et al., 2015
Amastra modicella Cooke, 1917	–	–	EX?	Régnier et al., 2015
Amastra moesta (Newcomb, 1854)	–	–	EX?	Régnier et al., 2015
Amastra montagui Pilsbry, 1913	–	–	EX?	Régnier et al., 2015
Amastra montana Baldwin, 1906	–	–	EX	Régnier et al., 2015
Amastra montivaga Cooke, 1917	–	–	EX?	Régnier et al., 2015
Amastra morticina Hyatt and Pilsbry, 1911*	–	–	EX	Régnier et al., 2015
Amastra mucronata (Newcomb, 1853)	–	–	EX?	Régnier et al., 2015
Amastra nana (Baldwin, 1895)	–	–	EX?	Régnier et al., 2015
Amastra nannodes Cooke, 1933	–	–	EX	Régnier et al., 2015
Amastra neglecta Pilsbry and Cooke, 1914	–	–	EX?	Régnier et al., 2015
Amastra nigra (Pfeiffer, 1856)	–	–	EX?	Régnier et al., 2015
Amastra nubifera Hyatt and Pilsbry, 1911	–	–	EX?	Régnier et al., 2015
Amastra nubigena Pilsbry and Cooke, 1914	–	–	EX?	Régnier et al., 2015
Amastra nubilosa (Mighels, 1845)	–	–	EX?	Régnier et al., 2015
Amastra nucleola (Gould, 1845)	–	–	EX	Régnier et al., 2015
Amastra nucula Smith, 1873	–	–	EX?	Régnier et al., 2015
Amastra obesa (Newcomb, 1853)	–	–	EX?	Régnier et al., 2015
Amastra oswaldi Cooke, 1933	–	–	EX?	Régnier et al., 2015
Amastra ovatula Cooke, 1933*	–	–	EX	Régnier et al., 2015
Amastra pagodula Cooke, 1917*	–	–	EX	Régnier et al., 2015
Amastra paulula Cooke, 1917	–	–	EX?	Régnier et al., 2015
Amastra peasei Smith, 1873	–	–	EX?	Régnier et al., 2015
Amastra pellucida (Baldwin, 1895)	EX 1994	EX	EX	Régnier et al., 2015
Amastra perversa Hyatt and Pilsbry, 1911*	–	–	EX	Régnier et al., 2015
Amastra petricola (Newcomb, 1855)	–	–	EX?	Régnier et al., 2015
Amastra pilsbryi Cooke, 1913	–	–	EX?	Régnier et al., 2015
Amastra porcus Hyatt and Pilsbry, 1911	EX 1994	EX	EX	Régnier et al., 2015
Amastra porpluyrostoma (Pease, 1869)	–	–	EX?	Régnier et al., 2015
Amastra praeopima Cooke, 1917	–	–	EX?	Régnier et al., 2015
Amastra problematica Cooke, 1933	–	–	EX?	Régnier et al., 2015
Amastra pullata (Baldwin, 1895)	–	–	EX?	Régnier et al., 2015
Amastra pusilla (Newcomb, 1854)	–	–	EX?	Régnier et al., 2015
Amastra reticulata (Newcomb, 1854)	EX 1994	EX	EX	Régnier et al., 2015
Amastra ricei Cooke, 1917	–	–	EX	Régnier et al., 2015
Amastra rubida Gulick, 1873	–	–	EX?	Régnier et al., 2015
Amastra rubristoma Baldwin, 1906	–	–	EX?	Régnier et al., 2015
Amastra rugulosa Pease, 1870	–	–	EX	Régnier et al., 2015
Amastra seminigra Hyatt and Pilsbry, 1911	–	–	EX	Régnier et al., 2015
Amastra seminuda Baldwin, 1906	–	–	EX?	Régnier et al., 2015
Amastra senilis Baldwin, 1903*	–	–	EX	Régnier et al., 2015
Amastra sericea (Pfeiffer, 1859	–	–	EX?	Régnier et al., 2015
Amastra similaris Pease, 1870	–	–	EX	Régnier et al., 2015
Amastra sinistrorsa Baldwin, 1906*	–	–	EX	Régnier et al., 2015
Amastra sola Hyatt and Pilsbry, 1911	–	–	EX?	Régnier et al., 2015
Amastra soror (Pfeiffer, 1868)	–	–	EX	Régnier et al., 2015
Amastra spaldingi Cooke, 1908	–	–	EX	Régnier et al., 2015
Amastra sphaerica Pease, 1870	–	–	EX	Régnier et al., 2015
Amastra spicula Cooke, 1917	–	–	EX?	Régnier et al., 2015
Amastra subcornea Hyatt and Pilsbry, 1911*	–	–	EX	Régnier et al., 2015
Amastra subcrassilabris Hyatt and Pilsbry, 1911	–	–	EX?	Régnier et al., 2015
Amastra subobscura Hyatt and Pilsbry, 1911	–	–	EX?	Régnier et al., 2015

(*Continued*)

Table A3. (cont.)

Species	Red List	Régnier et al., 2009	This study	Source for revised status; comments
Amastra subrostrata (Pfeiffer, 1859	EX 1994	EX	EX	Régnier et al., 2015
Amastra subsoror Hyatt and Pilsbry, 1911	EX 1994	EX	EX	Régnier et al., 2015
Amastra sykesi Hyatt and Pilsbry, 1911	–	–	EX?	Régnier et al., 2015
Amastra tenuilabris Gulick, 1873	–	–	EX?	Régnier et al., 2015
Amastra tenuispira (Baldwin, 1895)	EX 1994	EX	EX	Régnier et al., 2015
Amastra textilis (Férrusac, 1825)	–	–	EX?	Régnier et al., 2015
Amastra thaanumi Hyatt and Pilsbry, 1911	–	–	EX?	Régnier et al., 2015
Amastra thurstoni Cooke, 1917*	–	–	EX	Régnier et al., 2015
Amastra transversalis (Pfeiffer, 1856)	–	–	EX?	Régnier et al., 2015
Amastra tricincta Hyatt and Pilsbry, 1911	–	–	EX?	Régnier et al., 2015
Amastra tristis (Férrusac, 1825)	–	–	EX?	Régnier et al., 2015
Amastra turritela (Férrusac, 1821)	–	–	EX?	Régnier et al., 2015
Amastra ultima Pilsbry and Cooke, 1914	–	–	EX	Régnier et al., 2015
Amastra umbilicata (Pfeiffer, 1856)	EX 1996	EX	EX	Régnier et al., 2015
Amastra umbrosa (Baldwin, 1895)	–	–	EX?	Régnier et al., 2015
Amastra undata (Baldwin, 1895)	–	–	EX?	Régnier et al., 2015
Amastra uniplicata (Hartman, 1888)	–	–	EX?	Régnier et al., 2015
Amastra variegata (Pfeiffer, 1849)	–	–	EX?	Régnier et al., 2015
Amastra vetusta (Baldwin, 1895)*	–	–	EX	Régnier et al., 2015
Amastra violacea (Newcomb, 1853)	–	–	EX?	Régnier et al., 2015
Amastra viriosa Cooke, 1917	–	–	EX	Régnier et al., 2015
Amastra whitei Cooke, 1917	–	–	EX	Régnier et al., 2015
Arnsia petasus (Ancey, 1899)	–	–	EX?	Régnier et al., 2015
Carelia anceophila Cooke, 1931	EX 1990	EX	EX	Régnier et al., 2015
Carelia bicolor (Jay, 1839)	EX 1990	EX	EX	Régnier et al., 2015
Carelia cochlea (Reeve, 1849)*	EX 1990	EX	EX	Régnier et al., 2015
Carelia cumingiana (Pfeiffer, 1855)	EX 1990	EX	EX	Régnier et al., 2015
Carelia dolei Ancey, 1893*	EX 1990	EX	EX	Régnier et al., 2015
Carelia evelynae Cooke and Kondo, 1952*	EX 1990	EX	EX	Régnier et al., 2015
Carelia glossema Cooke, 1931	EX 1990	EX	EX	Régnier et al., 2015
Carelia hyattiana Pilsbry, 1911	EX 1990	EX	EX	Régnier et al., 2015
Carelia kalalauensis Cooke, 1931	EX 1990	EX	EX	Régnier et al., 2015
Carelia knudseni Cooke, 1931	EX 1990	EX	EX	Régnier et al., 2015
Carelia lirata Cooke, 1931*	EX 1990	EX	EX	Régnier et al., 2015
Carelia lymani Cooke, 1931*	EX 1990	EX	EX	Régnier et al., 2015
Carelia mirabilis Cooke, 1931*	EX 1990	EX	EX	Régnier et al., 2015
Carelia necra Cooke, 1931*	EX 1990	EX	EX	Régnier et al., 2015
Carelia olivacea Pease, 1866	EX 1990	EX	EX	Régnier et al., 2015
Carelia paradoxa (Pfeiffer, 1854)	EX 1990	EX	EX	Régnier et al., 2015
Carelia periscelis Cooke, 1931	EX 1990	EX	EX	Régnier et al., 2015
Carelia pilsbryi Sykes, 1909	EX 1990	EX	EX	Régnier et al., 2015
Carelia sinclairi Ancey, 1892*	EX 1990	EX	EX	Régnier et al., 2015
Carelia tenebrosa Cooke, 1931	EX 1990	EX	EX	Régnier et al., 2015
Carelia turricula (Mighels, 1845)	EX 1990	EX	EX	Régnier et al., 2015
Laminella alexandri (Newcomb, 1865)	–	–	EX	Régnier et al., 2015
Laminella bulbosa (Gulick, 1858)	–	–	EX?	Régnier et al., 2015
Laminella citrina (Pfeiffer, 1848)	–	–	EX?	Régnier et al., 2015
Laminella concinna (Newcomb, 1854)	–	–	EX?	Régnier et al., 2015
Laminella depicta (Baldwin, 1895)	–	–	EX?	Régnier et al., 2015
Laminella gravida (Férussac, 1825)	–	–	EX?	Régnier et al., 2015
Laminella kulnsi (Cooke, 1908)	–	–	EX?	Régnier et al., 2015
Laminella picta (Mighels, 1845)	–	–	EX?	Régnier et al., 2015
Laminella remyi (Newcomb, 1855)	–	–	EX?	Régnier et al., 2015
Laminella straminea (Reeve, 1850)	–	–	EX?	Régnier et al., 2015
Laminella tetrao (Newcomb, 1855)	–	–	EX?	Régnier et al., 2015
Laminella venusta (Mighels, 1845)	–	–	EX?	Régnier et al., 2015
Leptachatina accineta (Mighels, 1845)	–	–	EX?	Régnier et al., 2015
Leptachatina acuminata (Gould, 1847)	–	–	EX	Régnier et al., 2015

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Table A3. (cont.)

Species	Red List	Régnier et al., 2009	This study	Source for revised status; comments
Leptachatina anceyana Cooke, 1910	–	–	EX?	Régnier et al., 2015
Leptachatina antiqua Pease, 1870	–	–	EX	Régnier et al., 2015
Leptachatina approximans Ancey, 1897	–	–	EX?	Régnier et al., 2015
Leptachatina arborea Sykes, 1900	–	–	EX?	Régnier et al., 2015
Leptachatina attenuata Cooke, 1911	–	–	EX	Régnier et al., 2015
Leptachatina baldwini Cooke, 1910	–	–	EX?	Régnier et al., 2015
Leptachatina balteata Pease, 1870	–	–	EX	Régnier et al., 2015
Leptachatina brevicula (Pease, 1869)	–	–	EX	Régnier et al., 2015
Leptachatina callosa (Pfeiffer, 1857)	–	–	EX?	Régnier et al., 2015
Leptachatina captiosa Cooke, 1910	–	–	EX?	Régnier et al., 2015
Leptachatina cingula (Gould, 1847)	–	–	EX?	Régnier et al., 2015
Leptachatina compacta (Pease, 1869)	–	–	EX	Régnier et al., 2015
Leptachatina concolor Cooke, 1910	–	–	EX?	Régnier et al., 2015
Leptachatina conicoides Sykes, 1900	–	–	EX?	Régnier et al., 2015
Leptachatina conspicienda Cooke, 1910	–	–	EX?	Régnier et al., 2015
Leptachatina convexiuscula Sykes, 1900	–	–	EX?	Régnier et al., 2015
Leptachatina cookei Pilsbry, 1914	–	–	EX	Régnier et al., 2015
Leptachatina corneola (Pfeiffer, 1846)	–	–	EX?	Régnier et al., 2015
Leptachatina coruscans (Hartman, 1888)	–	–	EX?	Régnier et al., 2015
Leptachatina costulata (Gulick, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina costulosa Pease, 1870	–	–	EX?	Régnier et al., 2015
Leptachatina deceptor Cockerell, 1927*	–	–	EX	Régnier et al., 2015
Leptachatina defuncta Cooke, 1910*	–	–	EX	Régnier et al., 2015
Leptachatina dimidiata (Pfeiffer, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina dormitor Pilsbry and Cooke, 1914*	–	–	EX	Régnier et al., 2015
Leptachatina dulcis Cooke, 1911	–	–	EX	Régnier et al., 2015
Leptachatina emerita Sykes, 1900	–	–	EX?	Régnier et al., 2015
Leptachatina exilis (Gulick, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina exoptabilis Cooke, 1910*	–	–	EX	Régnier et al., 2015
Leptachatina extensa Pease, 1870	–	–	EX?	Régnier et al., 2015
Leptachatina fossilis Cooke, 1910*	–	–	EX	Régnier et al., 2015
Leptachatina fraterna Cooke, 1911	–	–	EX?	Régnier et al., 2015
Leptachatina fulgida Cooke, 1910	–	–	EX?	Régnier et al., 2015
Leptachatina fumida (Gulick, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina fusca (Newcomb, 1853)	–	–	EX?	Régnier et al., 2015
Leptachatina fuscula (Gulick, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina gayi Cooke, 1911	–	–	EX	Régnier et al., 2015
Leptachatina glutinosa (Pfeiffer, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina grana (Newcomb, 1853)	–	–	EX?	Régnier et al., 2015
Leptachatina guttula (Gould, 1847)	–	–	EX?	Régnier et al., 2015
Leptachatina haenensis Cockerell, 1927*	–	–	EX	Régnier et al., 2015
Leptachatina henshawi Sykes, 1903	–	–	EX	Régnier et al., 2015
Leptachatina hyperodon Pilsbry and Cooke, 1914*	–	–	EX	Régnier et al., 2015
Leptachatina illimis Cooke, 1910	–	–	EX?	Régnier et al., 2015
Leptachatina imitatrix Sykes, 1900*	–	–	EX	Régnier et al., 2015
Leptachatina impressa Sykes, 1896	–	–	EX?	Régnier et al., 2015
Leptachatina irregularis (Pfeiffer, 1856)	–	–	EX	Régnier et al., 2015
Leptachatina isthmica Ancey and Sykes, 1899*	–	–	EX	Régnier et al., 2015
Leptachatina knudseni Cooke, 1910	–	–	EX	Régnier et al., 2015
Leptachatina konaensis Sykes, 1900	–	–	EX	Régnier et al., 2015
Leptachatina kuhnsi Cooke, 1910	–	–	EX?	Régnier et al., 2015
Leptachatina labiata (Newcomb, 1853)	–	–	EX?	Régnier et al., 2015
Leptachatina laevigata Cooke, 1910	–	–	EX?	Régnier et al., 2015
Leptachatina laevis Pease, 1870	–	–	EX	Régnier et al., 2015
Leptachatina lagena (Gulick, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina lanaiensis Cooke, 1911	–	–	EX?	Régnier et al., 2015
Leptachatina lanceolata Cooke, 1911	–	–	EX?	Régnier et al., 2015
Leptachatina leiahiensis Cooke, 1910*	–	–	EX	Régnier et al., 2015

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Table A3. (cont.)

Species	Red List	Régnier et al., 2009	This study	Souree for revised status; comments
Leptachatina lenta Cooke, 1911	–	–	EX?	Régnier et al., 2015
Leptachatina leucochila (Gulick, 1856)	–	–	EX	Régnier et al., 2015
Leptachatina longiuscula Cooke, 1910	–	–	EX?	Régnier et al., 2015
Leptachatina lucida Pease, 1870	–	–	EX	Régnier et al., 2015
Leptachatina maniensis (Pfeiffer, 1855)	–	–	EX?	Régnier et al., 2015
Leptachatina marginata (Gulick, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina mcgregori Pilsbry and Cooke, 1914	–	–	EX	Régnier et al., 2015
Leptachatina microdon Pilsbry and Cooke, 1914	–	–	EX?	Régnier et al., 2015
Leptachatina molokaiensis Cooke, 1910	–	–	EX?	Régnier et al., 2015
Leptachatina morbida Cooke, 1911	–	–	EX?	Régnier et al., 2015
Leptachatina nematoglypta Pilsbry and Cooke, 1914)	–	–	EX?	Régnier et al., 2015
Leptachatina obsoleta (Pfeiffer, 1857)	–	–	EX	Régnier et al., 2015
Leptachatina obtusa (Pfeiffer, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina octogyrata (Gulick, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina omphalodes (Ancey, 1899)	–	–	EX?	Régnier et al., 2015
Leptachatina opipara Cooke, 1910	–	–	EX?	Régnier et al., 2015
Leptachatina optabilis Cooke, 1911	–	–	EX?	Régnier et al., 2015
Leptachatina oryza (Pfeiffer, 1856)*	–	–	EX	Régnier et al., 2015
Leptachatina ovata Cooke, 1910	–	–	EX?	Régnier et al., 2015
Leptachatina pachystoma (Pease, 1869)	–	–	EX	Régnier et al., 2015
Leptachatina perforata Cooke, 1911	–	–	EX?	Régnier et al., 2015
Leptachatina perkinsi Sykes, 1896	–	–	EX?	Régnier et al., 2015
Leptachatina petila (Gulick, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina pilsbryi Cooke, 1910	–	–	EX?	Régnier et al., 2015
Leptachatina praestabilis Cooke, 1910	–	–	EX?	Régnier et al., 2015
Leptachatina pulchra Cooke, 1910	–	–	EX?	Régnier et al., 2015
Leptachatina pumicata (Mighels, 1845)	–	–	EX?	Régnier et al., 2015
Leptachatina pupoidea Cooke, 1911	–	–	EX	Régnier et al., 2015
Leptachatina pyramis (Pfeiffer, 1846)	–	–	EX?	Régnier et al., 2015
Leptachatina resinula (Gulick, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina saccula (Hartman, 1888)	–	–	EX?	Régnier et al., 2015
Leptachatina sagittata Pilsbry and Cooke, 1914	–	–	EX	Régnier et al., 2015
Leptachatina sandwicensis (Pfeiffer, 1846)	–	–	EX?	Régnier et al., 2015
Leptachatina saxatilis (Gulick, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina sculpta (Pfeiffer, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina scutilus (Mighels, 1845)	–	–	EX?	Régnier et al., 2015
Leptachatina semipicta Sykes, 1896	–	–	EX?	Régnier et al., 2015
Leptachatina simplex (Pease, 1869)	–	–	EX	Régnier et al., 2015
Leptachatina smithi Sykes, 1896	–	–	EX?	Régnier et al., 2015
Leptachatina somniator Pilsbry and Cooke, 1914*	–	–	EX	Régnier et al., 2015
Leptachatina stiria (Gulick, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina striata (Newcomb, 1861)	–	–	EX?	Régnier et al., 2015
Leptachatina striatula (Gould, 1845)	–	–	EX	Régnier et al., 2015
Leptachatina subcylindracea Cooke, 1910*	–	–	EX	Régnier et al., 2015
Leptachatina subovata Cooke, 1910	–	–	EX?	Régnier et al., 2015
Leptachatina subula (Gulick, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina succincta (Newcomb, 1855)	–	–	EX?	Régnier et al., 2015
Leptachatina supracostata Sykes, 1900	–	–	EX?	Régnier et al., 2015
Leptachatina tenebrosa Pease, 1870	–	–	EX	Régnier et al., 2015
Leptachatina tenuicostata (Pease, 1869)*	–	–	EX	Régnier et al., 2015
Leptachatina terebralis (Gulick, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina teres (Pfeiffer, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina thaanumi Cooke, 1911	–	–	EX?	Régnier et al., 2015
Leptachatina triticea (Gulick, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina turrita (Gulick, 1856)	–	–	EX?	Régnier et al., 2015
Leptachatina vana Sykes, 1900	–	–	EX?	Régnier et al., 2015
Leptachatina varia Cooke, 1910	–	–	EX	Régnier et al., 2015
Leptachatina ventulus (Férussac, 1825)	–	–	EX?	Régnier et al., 2015

(*Continued*)

Table A3. (cont.)

Species	Red List	Régnier et al., 2009	This study	Source for revised status; comments
Pauahia artata (Cooke, 1911	–	–	EX?	Régnier et al., 2015
Pauahia chrysallis (Pfeiffer, 1855)	–	–	EX?	Régnier et al., 2015
Pauahia tantilla (Cooke, 1911)	–	–	EX?	Régnier et al., 2015
Planamastra digonomorpha (Ancey, 1889)	–	–	EX?	Régnier et al., 2015
Planamastra peaseana Pilsbry, 1911	–	–	EX?	Régnier et al., 2015
Planamastra spaldingi Cooke, 1933	–	–	EX?	Régnier et al., 2015
Tropidoptera alata (Pfeiffer, 1856)	–	–	EX	Régnier et al., 2015
Tropidoptera discus Pilsbry and Vanatta, 1905	–	–	EX	Régnier et al., 2015
Tropidoptera heliciformis (Ancey, 1890)	–	–	EX?	Régnier et al., 2015
Tropidoptera rex (Sykes, 1904)	–	–	EX?	Régnier et al., 2015
Tropidoptera wesleyi (Sykes, 1896)	–	–	EX?	Régnier et al., 2015
AMPHIBULIMULIDAE				
Eudolichotis euryomphala (Jonas, 1844)	–	EX?	EX?	
Eudolichotis sinuata (Albers, 1854)	–	EX?	EX?	
Plekocheilus pulicarius (Reeve, 1848)	–	EX?	EX?	
Plekocheilus succinoides (Petit, 1840)	–	EX?	EX?	
ANNULARIIDAE				
Parachondria basicarinata (Pfeiffer, 1855)	–	–	EX?	Watters, 2014
ARIOPHANTIDAE				
Ariophanta thyreus (Benson, 1852)	–	EX?	EX?	
Hemiplecta neptunus Pfeiffer, 1854	–	EX?	EX?	
Vitrinula chaunax (Pilsbry and Hirase, 1904)	EX 1994	–	EX	
Vitrinula chichijimana (Pilsbry and Hirase, 1905)	EX 1994	EX	EX	
Vitrinula hahajimana (Pilsbry and Hirase, 1905)	EX 1994	EX	EX	
ASSIMINEIDAE				
Conacmella vagans Hirase, 1907	–	EX	EX	
Cyclomorpha secessa Bouchet and Abdou, 2003	–	EX	EX	
Electrina succinea (Sowerby, 1846)	–	EX	EX	
Garrettia rotella (Pease, 1868)	–	–	EX?	Brook, 2010; F. Brook, pers. comm, 2016
Kubaryia pilikia Clench 1948	CR(PE) 2012	–	EX?	R.J. Rundell, pers. comm., 2016
Omphalotropis bassinblancensis Griffiths and Florens, 2004	–	EX	EX	
Omphalotropis dupontiana Nevill, 1878	–	EX	EX	
Omphalotropis ingens (Mousson, 1870)	CR(PE) 2012	–	EX?	
Omphalotropis margarita (Pfeiffer 1851)	–	EX	EX	
Omphalotropis maxima Madge, 1939	–	EX	EX	
Omphalotropis multilirata (Pfeiffer, 1852)	–	EX	EX	
Omphalotropis plicosa (Pfeiffer, 1852)	EX 1994	–	EX	
Omphalotropis quittorensis Griffiths and Florens, 2004	–	EX	EX	
Omphalotropis rotumana Smith, 1897	–	EX	EX	
Omphalotropis vacoasensis Griffiths and Florens, 2004	–	EX	EX	
BOTHRIEMBRYONTIDAE				
Leucocharis loyaltiensis (Souverbie, 1879)	EX 1994	EX	EX	
Leucocharis porphyrocheila (Dautzenberg and Bernier, 1901)	EX 1994	EX	EX	
Placostylus cuniculinsulae Cox, 1872	EX 1996	EX	EX	
Placostylus koroensis (Garrett, 1872)	CR(PE) 2012	EX?	EX?	
BRADYBAENIDAE				
Calocochlia cailliaudi Deshayes, 1839	–	EX?	EX?	
Calocochlia chlorochroa Sowerby, 1841	–	EX?	EX?	
Calocochlia cumingii Pfeiffer, 1842	–	EX?	EX?	
Chloraea fragilis (Sowerby, 1841)	–	EX?	EX?	
Euhadra murayamai Habe, 1976	DD	–	EX	Ministry of the Environment Government of Japan, 2016

(*Continued*)

Table A3. (cont.)

Species	Red List	Régnier et al., 2009	This study	Source for revised status; comments
Euhadra nachicola Kuroda, 1929	DD	–	EX	Ministry of the Environment Government of Japan, 2016
Euhadra sadoensis (Pilsbry and Hirase, 1903)	DD	–	EX	Ministry of the Environment Government of Japan, 2016
Helicostyla carbonaria (Sowerby, 1842)	–	EX?	EX?	
Helicostyla collodes (Sowerby 1841)	–	EX	EX	
Helicostyla cunctator (Reeve, 1849)	–	EX	EX	
Helicostyla daphnis (Broderip, 1841)	–	EX	EX	
Helicostyla moreleti (Pfeiffer, 1890)	–	EX	EX	
Helicostyla pfeifferi Semper, 1877	–	EX	EX	
Helicostyla phloiodes (Pfeiffer, 1842)	–	EX	EX	
Helicostyla pilsbryi (Hidalgo 1890)	–	EX	EX	
Helicostyla propitia (Fulton, H.C. 1907)	–	EX?	EX?	
Helicostyla velata (Broderip, 1841)	–	EX?	EX?	
Helicostyla zebuensis (Broderip, 1841)	–	EX?	EX?	
Mandarina luhuana (Sowerby, 1839)	–	EX	EX	
BULIMULIDAE				
Bulimulus achatellinus (Forbes, 1850)	CR(PE) 2003	–	EX?	
Bulimulus adelphus (Dall, 1917)	CR(PE) 2003	–	EX?	
Bulimulus brunoi von Ihering, 1917	–	EX	EX	
Bulimulus deridderi (Coppois, 1985)	CR(PE) 2003	–	EX?	
Bulimulus duncanus (Dall, 1893)	CR(PE) 2003	–	EX?	
Bulimulus eos (Odhner, 1951)	CR(PE) 2003	–	EX?	
Bulimulus lycodus (Dall, 1917)	CR(PE) 2003	–	EX?	
Bulimulus saeronius (Dall, 1917)	CR(PE) 2003	–	EX?	
Bulimulus tanneri (Dall, 1895)	CR(PE) 2003	–	EX?	
Naesiotus arnaldoi (Lanzieri and Rezende, 1971)	–	–	EX?	Salvador et al., 2013
CAMAENIDAE				
Aegista inexpecta Kuroda and Minato, 1977	–	EX	EX	
Amphidromus dohrni (Pfeiffer, 1863)	–	EX?	EX?	
Amphidromus metabletus Moellendorff, 1900	–	EX?	EX?	
Amphidromus sinensis (Benson, 1851)	–	EX?	EX?	
Satsuma fausta (Pilsbry, 1902)	–	–	EX	Association of Wildlife Research and EnVision Conservation Office, 2015
CERASTIDAE				
Pachnodus curiosus Gerlach, 2003	EX 2009	EX	EX	
Pachnodus ladiguensis Gerlach, 2003	EX 2009	EX	EX	
Pachnodus velutinus (Pfeiffer, 1868)	EX 2009	EX	EX	
Rachis comorensis (Morelet, 1881)	EX 1994	EX?	EX?	
Rachis sanguineus (Barclay, 1857)	EX 1994	EX	EX	
Rachistia vesiculatus (Benson, 1859)	–	EX	EX	
CHAROPIDAE				
Charopa perryi Smith, 1897	–	EX	EX	
Charopa rotumana Smith 1897	–	EX	EX	
Damonita geminoropiformis Climo, 1981	–	–	EX	Spencer et al., 2009
Discocharopa aperta (Moellendorff, 1888)	–	EX	EX	
Helenoconcha leptalea (Smith, 1892)	EX 1994	EX	EX	
Helenoconcha minutissima (Smith, 1892)	EX 1994	EX	EX	
Helenoconcha polyodon (Sowerby, 1844)	EX 1994	EX	EX	
Helenoconcha pseustes (Smith, 1892)	EX 1994	EX	EX	
Helenoconcha sexdentata (Smith, 1893)	EX 1994	EX	EX	
Helenodiscus bilamellata (Sowerby, 1844)	EX 1994	EX	EX	
Helenodiscus vernoni (Smith 1892)	EX 1994	EX	EX	
Hirasea biconcava Hirase, 1907	–	EX	EX	
Hirasea diplomphalus Pilsbry, 1902	–	EX	EX	
Hirasea eutheca Hirase, 1907	–	EX	EX	
Hirasea goniobasis Pilsbry, 1902	–	EX	EX	
Hirasea hypolia Hirase, 1907	–	EX	EX	

(*Continued*)

Table A3. (cont.)

Species	Red List	Régnier et al., 2009	This study	Source for revised status; comments
Hirasea insignis Pilsbry and Hirase, 1904	EN	–	EX	Ministry of the Environment Government of Japan, 2016
Hirasea major Pilsbry, 1902	–	EX	EX	
Hirasea operculina (Gould, 1859)	EN	–	EX	Ministry of the Environment Government of Japan, 2016
Hirasea sinuosa Pilsbry, 1902	–	EX	EX	
Lauopa mbalavuana Solem, 1983	CR(PE) 2012	–	EX?	
Libera subcavernula (Tryon, 1887)	EX 1994	EX	EX	
Libera tumuloides (Garrett, 1872)	EX 1994	EX	EX	
Mautodontha acuticosta (Garrett, 1884)	EX 1994	EX	EX	
Mautodontha consimilis (Pease, 1868)	EX 1994	EX	EX	
Mautodontha consobrina (Garrett, 1884)	EX 1994	EX	EX	
Mautodontha maupiensis (Garrett, 1872)	EX 1994	EX	EX	
Mautodontha parvidens (Pease, 1861)	EX 1994	EX	EX	
Mautodontha punctiperforata (Garrett, 1884)	EX 1994	EX	EX	
Mautodontha saintjohni Solem, 1976	EX 1994	EX	EX	
Mautodontha subtilis (Garrett, 1884)	EX 1994	EX	EX	
Mautodontha unilamellata (Garrett, 1874)	EX 1994	EX	EX	
Mautodontha zebrina (Garrett, 1874)	EX 1994	EX	EX	
Mocella elliottae (Climo, 1969)	–	–	EX	Spencer et al., 2009
Mocella spelaeus (Climo, 1971)	–	–	EX	Spencer et al., 2009
Propilula cyclaria (Morelet, 1875)	–	EX	EX	
Sinployea canalis (Garrett, 1872)	EX 1994	EX	EX	
Sinployea decorticata (Garrett, 1872)	EX 1994	EX	EX	
Sinployea harveyensis (Garrett, 1872)	EX 1994	EX	EX	
Sinployea muri Brook, 2010	–	–	EX	Brook, 2010; F. Brook, pers. comm, 2016
Sinployea otareae (Garrett, 1872)	EX 1994	EX	EX	
Sinployea planospira (Garrett, 1881)	EX 1994	EX	EX	
Sinployea proxima (Garrett, 1872)	EX 1994	EX	EX	
Sinployea rudis (Garrett, 1872)	EX 1994	EX	EX	
Sinployea tenuicostata (Garrett, 1872)	EX 1994	EX	EX	
Sinployea titikaveka Brook, 2010	–	EX?	EX	Brook, 2010; F. Brook, pers. comm, 2016
Sinployea tupapa Brook, 2010	–	EX?	EX	Brook, 2010; F. Brook, pers. comm, 2016
Sinployea youngi (Garrett, 1872)	EX 1994	EX	EX	
Taipidon anceyana (Garrett, 1887)	EX 1994	EX	EX	
Taipidon marquesana (Garrett, 1887)	EX 1994	EX	EX	
Taipidon octolamellata (Garrett, 1887)	EX 1994	EX	EX	
Trachycystis rariplicata (Benson, 1887)	–	EX	EX	
Zelandiscus elevatus (Climo, 1978)	–	–	EX	Climo, 1981
CHRONIDAE				
Trochochlamys ogasawarana (Pilsbry, 1902)	–	EX	EX	
CLAUSILIDAE				
Neophaedusa spelaeonis Kuroda and Minato, 1975	DD	DD?	EX	Ministry of the Environment Government of Japan, 2016
COCHLICELLIDAE				
Monilearia pulverulenta (Lowe, 1861)	CR(PE) 2011	–	EX?	
CYCLOPHORIDAE				
Cyclophorus acutimarginatus (Sowerby, 1842)	–	EX?	EX?	
Cyclophorus stenomphalus (Pfeiffer, 1846)	–	EX?	EX?	
Nobuea kurodai Minato and Tada, 1978	DD 1996	–	EX	Ministry of the Environment Government of Japan, 2016
DIPLOMMATINIDAE				
Diplommatina alata (Crosse 1866)	CR(PE) 2012	–	EX?	R.J. Rundell, pers. comm., 2016
Diplommatina aurea Beddome 1889	CR(PE) 2012	–	EX?	R.J. Rundell, pers. comm., 2016

(*Continued*)

Table A3. (cont.)

Species	Red List	Régnier et al., 2009	This study	Source for revised status; comments
Diplommatina gibboni Beddome 1889	CR(PE) 2012	–	EX?	R.J. Rundell, pers. comm., 2016
Opisthostoma decrespignyi (H. Adams, 1865)	CR(PE) 2004	EX?	EX?	
Opisthostoma otostoma Boettger, 1893	CR(PE) 2004	EX?	EX?	
Palaina albata (Beddome 1889)	CR(PE) 2012	–	EX?	R.J. Rundell, pers. comm., 2016
Palaina patula (Crosse 1866)	CR(PE) 2012	–	EX?	R.J. Rundell, pers. comm., 2016
Palaina platycheilus (Beddome 1889)	CR(PE) 2012	–	EX?	R.J. Rundell, pers. comm., 2016
Palaina pupa Crosse 1866	CR(PE) 2012	–	EX?	R.J. Rundell, pers. comm., 2016
Plectostoma charasense (Tomlin, 1948)	CR(PE) 2014	–	EX?	
Plectostoma dindingense Liew et al., 2014	CR(PE) 2014	–	EX?	
Plectostoma sciaphilum (van Benthem Jutting, 1952)	EX 2014	–	EX	Schilthuizen and Clements, 2008; Liew et al., 2014
Plectostoma turriforme (van Benthem Jutting, 1952)	CR(PE) 2014	–	EX?	
DISCIDAE				
Keraea garachicoensis (Wollaston 1878)	–	EX	EX	
DYAKIIDAE				
Dyakia clippeus (Mousson, 1849)	–	EX?	EX?	
ENDODONTIDAE				
Aaadonta angaurana Solem 1976	CR(PE) 2012	–	EX?	R.J. Rundell, pers. comm., 2016
Aaadonta kinlochi Solem 1976	CR(PE) 2012	–	EX?	R.J. Rundell, pers. comm., 2016
Aaadonta pelewana Solem 1976	CR(PE) 2012	–	EX?	R.J. Rundell, pers. comm., 2016
Anceyodonta alternata Cooke and Solem, 1976	–	EX	EX	
Anceyodonta andersoni Cooke and Solem, 1976	–	EX	EX	
Anceyodonta constricta Cooke and Solem, 1976	–	EX	EX	
Anceyodonta densicostata Cooke and Solem, 1976	–	EX	EX	
Anceyodonta difficilis Solem, 1976	–	EX	EX	
Anceyodonta ganlutuensis Cooke and Solem, 1976	–	EX	EX	
Anceyodonta gatavakensis Abdou and Bouchet, 2000	–	EX	EX	
Anceyodonta hamyana (Ancey, 1889)	–	EX	EX	
Anceyodonta labiosa Solem, 1976	–	EX	EX	
Anceyodonta obesa Solem, 1976	–	EX	EX	
Anceyodonta sexlamellata (Pfeiffer, 1845)	–	EX	EX	
Anceyodonta soror Solem, 1976	–	EX	EX	
Anceyodonta subconica Solem and Cooke, 1976	–	EX	EX	
Anceyodonta umbilicata Abdou and Bouchet, 2000	–	EX	EX	
Australdonta anneae Sartori et al., 2013	–	–	EX	Sartori et al., 2013
Australdonta collicella Zimmermann et al., 2009	–	–	EX	
Australdonta ectopia Solem, 1976	–	EX	EX	
Australdonta florencei Sartori et al., 2013	–	–	EX	Sartori et al., 2013
Australdonta magnasulcatissima Zimmermann et al., 2009	–	–	EX	Zimmerman et al., 2009
Australdonta microspiralis Zimmermann et al., 2009	–	–	EX	Zimmermann et al., 2009
Australdonta oleatora Sartori, Gargominy and Fontaine, 2013	–	–	EX	Sartori et al., 2013
Australdonta pakalolo Sartori, Gargominy and Fontaine, 2013	–	–	EX	Sartori et al., 2013
Australdonta pharcata Solem, 1976	–	EX	EX	
Australdonta pseudplanulata Solem, 1976	–	EX	EX	
Australdonta rimatarana Solem, 1976	–	EX	EX	
Australdonta sibleti Sartori et al., 2013	–	–	EX	Sartori et al., 2013
Australdonta sulcata Zimmermann et al., 2009	–	–	EX	Zimmermann et al., 2009
Australdonta teaae Sartori et al., 2013	–	–	EX	Sartori et al., 2013
Australdonta tubuaiana Solem, 1976	–	EX	EX	
Endodonta apiculata (Ancey, 1889)	CR(PE) 2000	–	EX?	
Gambiodonta agakauitaiana Solem and Cooke, 1976	–	EX	EX	
Gambiodonta grandis Cooke and Solem, 1976	–	EX	EX	
Gambiodonta mangarevana Solem and Cooke, 1976	–	EX	EX	
Gambiodonta mirabilis Cooke and Solem, 1976	–	EX	EX	

(*Continued*)

Table A3. (cont.)

Species	Red List	Régnier et al., 2009	This study	Source for revised status; comments
Gambiodonta pilsbryi Cooke and Solem, 1976	–	EX	EX	
Gambiodonta tumida Cooke and Solem, 1976	–	EX	EX	
Hirasea planulata Pilsbry and Hirase, 1903	EX 1994	EX	EX	
Kleokyphus callinus Solem, 1976	–	–	EX	Sartori et al., 2014
Kleokyphus cowiei Sartori et al., 2014	–	–	EX	Sartori et al., 2014
Kleokyphus hypsus Solem, 1976	–	–	EX	Sartori et al., 2014
Mautodontha aurora Sartori et al., 2014	–	–	EX	Sartori et al., 2014
Mautodontha ceuthma Solem, 1976	–	EX	EX	
Mautodontha domaneschii Sartori et al., 2014	–	–	EX	Sartori et al., 2014
Mautodontha harperae Sartori et al., 2014	–	–	EX	Sartori et al., 2014
Mautodontha makateaensis Sartori et al., 2014	–	–	EX	Sartori et al., 2014
Mautodontha occidentalis Sartori et al., 2014	–	–	EX	Sartori et al., 2014
Mautodontha passosi Sartori et al., 2014	–	–	EX	Sartori et al., 2014
Mautodontha rarotongensis (Pease, 1870)	–	–	EX[?]	Brook et al., 2010; F. Brook, pers. comm., 2016
Mautodontha spelunca Sartori et al., 2014	–	–	EX	Sartori et al., 2014
Mautodontha temaoensis Sartori et al., 2014	–	–	EX	Sartori et al., 2014
Mautodontha virginiae Sartori et al., 2014	–	–	EX	Sartori et al., 2014
Minidonta anatonuana Solem, 1976	–	EX	EX	
Minidonta aroa Brook, 2010	–	–	EX	Brook, 2010; F. Brook, pers. comm., 2016
Minidonta arorangi Brook, 2010	–	–	EX	Brook, 2010; F. Brook, pers. comm., 2016
Minidonta bieleri Sartori et al., 2013	–	–	EX	Sartori et al., 2013
Minidonta boucheti Sartori et al., 2013	–	–	EX	Sartori et al., 2013
Minidonta extraria Cooke and Solem, 1976	–	EX	EX	
Minidonta flammulina Abdou and Bouchet, 2000	–	EX	EX	
Minidonta gravacosta Solem, 1976	–	EX	EX	
Minidonta haplaenopla Solem, 1976	–	EX	EX	
Minidonta iota Brook, 2010	–	–	EX	Brook, 2010; F. Brook, pers. comm., 2016
Minidonta kavera Brook, 2010	–	–	EX	Brook, 2010; F. Brook, pers. comm., 2016
Minidonta macromphalus Preece, 1998	–	EX	EX	
Minidonta manuaensis Solem, 1976	–	EX	EX	
Minidonta micra Solem and Cooke, 1976	–	EX	EX	
Minidonta micraconica Solem, 1976	–	EX	EX	
Minidonta ngatangiia Brook, 2010	–	–	EX	Brook, 2010; F. Brook, pers. comm., 2016
Minidonta perminima Abdou and Bouchet, 2000	–	EX	EX	
Minidonta planulata Solem, 1976	–	EX	EX	
Minidonta pue Brook, 2010	–	–	EX	Brook, 2010; F. Brook, pers. comm., 2016
Minidonta rutaki Brook, 2010	–	–	EX	Brook, 2010; F. Brook, pers. comm., 2016
Minidonta simulata Solem and Cooke, 1976	–	EX	EX	
Minidonta sulcata Solem, 1976	–	EX	EX	
Minidonta taravensis Solem and Cooke, 1976	–	EX	EX	
Minidonta taunensis Solem and Cooke, 1976	–	EX	EX	
Minidonta vallonia Abdou and Bouchet, 2000	–	EX	EX	
Pseudohelenoconcha spurca (Sowerby, 1844)	EX 1994	EX	EX	
Pseudolibera aubertdelaruei Sartori et al., 2014	–	–	EX	Sartori et al., 2014
Pseudolibera cookei Sartori et al., 2014	–	–	EX	Sartori et al., 2014
Pseudolibera elieporoii Sartori et al., 2014	–	–	EX	Sartori et al., 2014
Pseudolibera extincta Sartori et al., 2014	–	–	EX	Sartori et al., 2014
Pseudolibera lillianae Solem, 1976	–	–	EX	Sartori et al., 2014
Pseudolibera matthieui Sartori et al., 2014	–	–	EX	Sartori et al., 2014
Pseudolibera paraminderae Sartori et al., 2014	–	–	EX	Sartori et al., 2014

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Table A3. (cont.)

Species	Red List	Régnier et al., 2009	This study	Source for revised status; comments
Pseudolibera parva Sartori et al., 2014	–	–	EX	Sartori et al., 2014
Pseudolibera solemi Sartori et al., 2014	–	–	EX	Sartori et al., 2014
Rikitea insolens Cooke and Solem, 1976	–	EX	EX	
Rikitea tapinoptyx Abdou and Bouchet, 2000	–	EX	EX	
Thaumatodon multilamellata (Garrett, 1872)	EX 1994	EX	EX	
ENIDAE				
Mirus hachijoensis (Kuroda, 1945)	DD	–	EX	Ministry of the Environment Government of Japan, 2016
EUCONULIDAE				
Advena campbelli (Gray, 1834)	EX 1996	EX	EX	
Aukena endodonta Bouchet and Abdou, 2001	–	EX	EX	
Aukena tridentata (Baker, 1940)	–	EX	EX	
Coneuplecta turrita (Semper, 1873)	CE(PE) 2012	–	EX?	
Cookeana anathesis Baker, 1938	–	EX	EX	
Cookeana vindex Baker, 1938	–	EX	EX	
Diastole matafaoi Baker, 1938	EX 1996	–	EX	
Diastole rurutui Baker, 1938	–	EX	EX	
Fanulena perrugosa Iredale, 1945	EX 1996	EX	EX	
Lamprocystis rurutuana Baker, 1938	–	EX	EX	
Microcystis adusta Baker, 1938	–	EX	EX	
Microcystis andersoni Baker, 1938	–	EX	EX	
Microcystis kondoi Baker, 1938	–	EX	EX	
Nancibella quintalia (Cox, 1870)	EX 1996	EX	EX	
Philonesia pyramidalis Preece, 1998	–	EX	EX	
Philonesia weisleri Preece, 1998	–	EX	EX	
Quintalia flosculus Cox, 1866	EX 1996	EX	EX	
Quintalia stoddartii Gray, 1834	EX 1996	EX	EX	
GASTROCOPTIDAE				
Campolaemus perexilis (Smith, 1892)	EX 1994	EX	EX	
Gastrocopta chichijimana Pilsbry, 1916	EX 1994	–	EX	
Gastrocopta ogasawarana Pilsbry, 1916	EX 1994	–	EX	
GASTRODONTIDAE				
Atlantica engonata (Shuttleworth, 1852)	–	EX	EX	
Atlantica retexta (Shuttleworth, 1852)	–	EX	EX	
Atlantica textilis (Shuttleworth, 1852)	–	EX	EX	
Janulus pompylius (Shuttleworth, 1852)	–	EX	EX	
Poecilozonites reinianus (Pfeiffer, 1863)	–	EX	EX	
HELICARIONIDAE				
Caldwellia philyrina Morelet, 1873	EX 1996	–	EX	
Ctenoglypta newtoni (Nevill, 1871)	EX 1994	EX	EX	
Ctenophila aigretteianum Griffiths, 2000	–	EX	EX	
Dancea bewsheriana (Morelet, 1875)	–	EX	EX	
Dupontia affouchensis Griffiths, 2000	–	EX	EX	
Dupontia proletaria (Morelet, 1860)	EX 1996	–	EX	
Epiglypta howinsulae (Cox, 1873)	–	EX	EX	
Erepta chloritiformis Griffiths and Vincent, 2004	–	EX	EX	
Erepta nevilli (H. Adams, 1867)	EX 1994	EX	EX	
Erepta pyramidalis Griffiths and Florens, 2004	–	EX	EX	
Erepta thiriouxi (Germain, 1918)	–	EX	EX	
Erepta wendystrahmi Griffiths, 2000	–	EX	EX	
Harmogenanina linophora (Morelet, 1860)	EX 1994	–	EX	
Harmogenanina subdetecta Germain, 1921	EX 1994	–	EX	
Hirasiella clara Pilsbry, 1902	–	EX	EX	
Pachystyla rufozonata (H. Adams), 1867	EX 1994	–	EX	
Pachystyla waynepagei Griffiths, 2000	–	EX	EX	
Plegma duponti (Morelet, 1866)	–	EX	EX	
Pseudophasis nevilli (H. Adams, 1867)	–	EX	EX	
HELICIDAE				

(*Continued*)

Table A3. (cont.)

Speeies	Red List	Régnier et al., 2009	This study	Source for revised status; comments
Hemicycla modesta (Férussac, 1821)	CR(PE) 2011	–	EX?	
HELICINIDAE				
Alcadia guadeloupensis (Sowerby, 1842)	–	EX	EX	
Nesiocina abdoui Richling and Bouchet, 2013	–	–	EX	Richling and Bouchet, 2013
Nesiocina gambierensis Richling and Bouchet, 2013	–	–	EX	Richling and Bouchet, 2013
Nesiocina grohi Richling and Bouchet, 2013	–	–	EX	Richling and Bouchet, 2013
Nesiocina mangarevae Richling and Bouchet, 2013	–	–	EX	Richling and Bouchet, 2013
Nesiocina pauciplicata Richling and Bouchet, 2013	–	–	EX	Richling and Bouchet, 2013
Nesiocina pazi (Crosse 1865)	–	–	EX	Richling and Bouchet, 2013
Nesiocina superoperculata Richling and Bouchet, 2013	–	–	EX	Richling and Bouchet, 2013
Nesiocina trilamellata Richling and Bouchet, 2013	–	–	EX	Richling and Bouchet, 2013
Nesiocina unilamellata Richling and Bouchet, 2013	–	–	EX	Richling and Bouchet, 2013
Ogasawarana arata Pilsbry, 1902	DD	–	EX	Ministry of the Environment Government of Japan, 2016
Ogasawarana capsula Pilsbry, 1902	DD	–	EX	Ministry of the Environment Government of Japan, 2016
Ogasawarana chichijimana Minato, 1980	–	EX	EX	
Ogasawarana discrepans Pilsbry, 1902	DD	–	EX	Ministry of the Environment Government of Japan, 2016
Ogasawarana habei Minato, 1980	–	EX	EX	
Ogasawarana metamorpha Minato, 1980	–	EX	EX	
Ogasawarana nitida Minato, 1980	DD	–	EX	Ministry of the Environment Government of Japan, 2016
Ogasawarana rex Minato, 1980	–	EX	EX	
Orobophana carinacosta Preece, 1998	–	EX	EX	
Pleuropoma hendersoni Preece, 1998	–	EX	EX	
Pseudotrochatella undulata (Morelet, 1878)	–	EX	EX	
HOLOSPIRIDAE				
Holospira piloceri (Pfeiffer, 1841)	–	EX	EX	
Coelostemma richardi Thompson, 1971	–	EX	EX	
HYGROMIIDAE				
Discula lyelliana (Lowe, 1852)	CR(PE) 2011	EX	EX?	
Discula tetrica (Lowe, 1852)	CR(PE) 2011	–	EX?	
Geomitra delphinuloides (Lowe, 1860)	CR(PE) 2011	–	EX?	
Geomitra grabhami (Wollaston, 1878)	CR(PE) 2011	EX	EX?	
Helicopsis paulhessei (Lindholm, 1936)	EX 2011	–	EX	
Montserratina becasis (Rambur, 1868)	CR(PE) 2011	–	EX?	
Pseudocampylaea loweii (Férussac, 1835)	EX 1996	EX	EX	
Trochoidea picardi (Haas, 1955)	EX 1996	EX	EX	
LAURIIDAE				
Leiostyla abbreviata Lowe, 1852	CR(PE) 2011	–	EX?	
Leiostyla cassida (Lowe, 1831)	CR(PE) 2011	–	EX?	
Leiostyla gibba Lowe, 1852	CR(PE) 2011	–	EX?	
Leiostyla lamellosa Lowe, 1852	EX 2011	EX	EX	
Leiostyla simulator (Pilsbry, 1923)	CR(PE) 2011	–	EX?	
MEGALOMASTOMATIDAE				
Madgeaconcha sevathiani Griffiths and Florens, 2004	CR(PE) 2014	EX	EX?	
NEOCYCLOTIDAE				
Amphicyclotulus guadeloupensis de la Torre, et al., 1942	EX 1996	EX	EX	
Incerticyclus cinereus (Drouët, 1859)	EX 1996	EX	EX	
ODONTOSTOMIDAE				
Tomigerus gibberulus (Burrow, 1815)	EX 1996	EX	EX	
Tomigerus turbinatus (Pfeiffer, 1845)	EX 1996	EX	EX	
OLEACINIDAE				
Oleacina guadeloupensis (Pfeiffer, 1857)	EX 1996	EX	EX	

(*Continued*)

Table A3. (cont.)

Species	Red List	Régnier et al., 2009	This study	Souree for revised status; comments
Oleacina paivana (Pfeiffer, 1866)	–	EX?	EX?	
OREOHELICIDAE				
Oreohelix florida Pilsbry, 1939	–	EX	EX	
PARMACELLIDAE				
Cryptella tamaranensis Hutterer, 1990	–	EX?	EX?	
Parmacella gervaisii Moquin-Tandon, 1850	–	EX	EX	
PARTULIDAE				
Eua globosa Pilsbry and Cooke, 1934	CR(PE) 2012	–	EX?	
Palaopartula leucothoe (Semper, 1865)	CR(PE) 2012	–	EX?	
Partula arguta (Pease, 1866)	EX 1996	EX	EX	
Partula atilis Crampton, 1956	EX 1994	EX	EX	
Partula aurantia Crampton, 1932	EX 1988	EX	EX	
Partula auriculata Broderip, 1832	EX 1994	EX	EX	
Partula bilineata Pease, 1866	EX 1996	EX	EX	
Partula clarkei Gerlach, 2016	–	–	EX	Gerlach, 2016
Partula cootei Gerlach, 2016	–	–	EX	Gerlach, 2016
Partula crassilabris Pease, 1866	EX 1994	EX	EX	
Partula cuneata Crampton, 1956	EX 1994	EX	EX	
Partula cytherea Cooke and Crampton, 1930	EX 1996	EX	EX?	Gerlach, 2016
Partula dentifera Pfeiffer, 1853	EW 1996	EW	EX	Gerlach, 2016
Partula desolata Bauman and Kerr, 2013*	–	–	EX	Bauman and Kerr, 2013; Gerlach, 2016
Partula diminuta Adams, 1851	–	–	EX	Gerlach, 2016
Partula dolichostoma Crampton, 1956	EX 1994	EX	EX	
Partula dolorosa Crampton and Cooke, 1953	EX 1996	EX	EX	
Partula eremita Crampton and Cook, 1953	EX 1996	EX	EX	
Partula faba (Gmelin, 1791)	EW 1996	EW	EX	Gerlach, 2016
Partula garrettii Pease, 1865	EX 2009	EW	EW	
Partula guamensis (Pfeiffer, 1846)	CR(PE) 2012	–	EX	Gerlach, 2016
Partula hebe (Pfeiffer, 1846)	EW 1996	EW	EW	
Partula jackieburchi (Kondo, 1981)	EX 1996	EX	EX	
Partula labrusca Crampton and Cooke, 1953	EX 2009	EW	EW	Gerlach, 2016
Partula langfordi Kondo, 1970	CR 1996	–	EX	Kerr, 2013; Bauman and Kerr, 2013; Gerlach, 2016
Partula leptochila Crampton, 1956	EX 1994	EX	EX	
Partula levistriata Crampton, 1956	EX 1994	EX	EX	
Partula lugubris Pease, 1865	EX 2009	EX	EX	
Partula lutea Lesson, 1831	EX 1994	EX	EX	
Partula magistri Gerlach, 2016	–	–	EX	Gerlach, 2016
Partula makatea Gerlach, 2016*	–	–	EX	Gerlach, 2016
Partula mirabilis Crampton, 1924	EW 1996	–	EW	
Partula mooreana Hartman, 1880	EW 1996	EW	EW	
Partula navigatoria (Pfeiffer, 1849)	EX 2009	EX	EW	Gerlach, 2016
Partula pearcekellyi Gerlach, 2016	–	–	EX	Gerlach, 2016
Partula planilabrum Pease, 1864	EX 1996	EX	EX	
Partula producta Pease, 1865	EX 1994	EX	EX	
Partula protracta Crampton, 1956	EX 1994	EX	EX	
Partula remota Crampton, 1956	EX 1994	EX	EX	
Partula rosea Broderip, 1832	EW 2009	–	EW	
Partula rufa Lesson, 1831	–	–	EX?	Gerlach, 2016
Partula sagitta Crampton and Cooke, 1953	EX 1996	EX	EX	
Partula salifana Crampton, 1925	EX 1994	EX	EX	
Partula suturalis Pfeiffer, 1855	EW 2009	EW	EW	
Partula tohiveana Crampton, 1924	EW 1996	EW	EW	
Partula tristis Crampton and Cooke, 1953	EW 1996	EW	EX	Gerlach, 2016
Partula turgida (Pease, 1865)	EX 1994	EX	EX	
Partula umbilicata Pease, 1866	EX 1996	EX	EX	
Partula varia Broderip, 1832	EW 2009	EX	EW	Gerlach, 2016

(*Continued*)

Table A3. (cont.)

Species	Red List	Régnier et al., 2009	This study	Source for revised status; comments
Samoana cramptoni Pilsbry and Cooke, 1934	CR(PE) 2012	–	EX?	
Samoana minuta (Pfeiffer, 1856)	–	–	EX?	Gerlach, 2016
Samoana pilsbryi Gerlach, 2016	–	–	EX?	Gerlach, 2016
PLEURODONTIDAE				
Discolepis desidens (Rang, 1834)	EX 1996	EX	EX	
Polydontes perplexa (Pfeiffer, 1850)	–	EX?	EX?	
Polydontes undulata (Férussac, 1821)	–	EX?	EX?	
POLYGYRIDAE				
Vespericola ohlone Roth, 2003	–	–	EX?	Roth, 2003
POMATIIDAE				
Tropidophora carinata (Born, 1780)	–	EX	EX	
Tropidophora desmazuresi (Crosse, 1873)	EX 1994	–	EX	
Tropidophora icterica (Sowerby, 1847)	–	EX	EX	
Tropidophora lienardi Morelet, 1876	–	EX	EX	
Tropidophora mauritiana (H. Adams, 1867)	–	EX	EX	
Tropidophora scabra (H.Adams, 1867)	–	EX	EX	
Tropidophora semilirata (Morelet, 1881)	EX 1994	–	EX	Evaluated as *Tropidophora 'semilineata'* by IUCN (2016)
Tropidophora vincentflorensi Griffiths, 2000	–	EX	EX	
PRISTILOMATIDAE				
Gyralina hausdorfi Riedel, 1990	–	EX	EX	
PUNCTIDAE				
Punctum mokotoense Abdou and Bouchet, 2000	–	EX	EX?	Abdou and Bouchet, 2000
PUPILLIDAE				
Pupilla obliquicosta Smith, 1892	EX 1994	EX	EX	
RHYTIDIDAE				
Delos gardineri Smith, 1897	CR(PE) 2012	EX	EX?	Barker, 2012
Schizoglossa major Powell, 1938	–	–	EX	Spencer et al., 2009
STREPTAXIDAE				
Conturbatia crenata Gerlach, 2001	CR(PE) 2009	–	EX?	
Gibbus lyonetianus Pallas, 1780	EX 1994	EX	EX	
Gonidomus newtoni (Adams, 1867)	EX 1994	EX	EX	
Gonospira adamsiana Nevill, 1871	–	EX	EX	
Gonospira cirueensis Madge, 1946	–	EX	EX	
Gonospira helodes (Morelet, 1875)	–	EX	EX	
Gonospira majuscula (Morelet, 1878)	–	EX	EX	
Gonospira mondraini (H. Adams, 1868)	–	EX	EX	
Gonospira nevilli Adams, 1867	EX 1994	–	EX	
Gulella mamellensis Griffiths, 2000	–	EX	EX	
Microstrophia abnormala Griffiths, 2004	–	EX	EX	
Microstrophia baideri Griffiths, 2004	–	EX	EX	
Plicadomus newtoni (H. Adams, 1867)	–	EX	EX	
STROPHOCHEILIDAE				
Anthinus multicolor Rang, 1831	–	EX?	EX?	
Anthinus turnix (Gould 1846)	–	EX?	EX?	
Gonyostomus egregius (Pfeiffer, 1845)	–	EX?	EX?	
Gonyostomus goniostoma (Wood, 1828)	–	EX?	EX?	
Megalobulimus cardosoi (Morretes, 1952)	EX 1996	EX	EX	
SUBULINIDAE				
Chilonopsis blofeldi Forbes, 1852	EX 1994	EX	EX	
Chilonopsis exulatus (Benson, 1850)	EX 1994	EX	EX	
Chilonopsis helena Quoy and Gaimard, 1833	EX 1994	EX	EX	
Chilonopsis melanoides (Wollaston, 1892)	EX 1996	EX	EX	
*Chilonopsis nonpareil** (Perry, 1811)	EX 1994	EX	EX	
Chilonopsis subplicatus (Sowerby, 1852)	EX 1994	EX	EX	
Chilonopsis subtruncatus (Smith, 1892)	EX 1994	EX	EX	
Chilonopsis turtoni (Smith, 1892)	EX 1994	EX	EX	
Vegrandinia trindadensis (Breure and Coelho, 1976)	–	–	EX?	

(*Continued*)

Table A3. (cont.)

Species	Red List	Régnier et al., 2009	This study	Source for revised status; comments
SUCCINEIDAE				
Succinea atollica Hertlein and Allison, 1968	–	EX	EX	
Succinea rotumana Smith, 1897	CR(PE) 2012	EX	EX?	Barker, 2012
UROCOPTIDAE				
Anoma adamsi Pilsbry, 1904	–	EX?	EX?	
Anoma alboanfractus (Chitty, 1853)	–	EX?	EX?	
Anoma dohriana (Pfeiffer, 1871)	–	EX?	EX?	
Anoma flexuosa (Pfeiffer, 1866)	–	EX?	EX?	
Anoma fuscolabris (Chitty, 1853)	–	EX?	EX?	
Anoma gossei (Pfeiffer, 1846)	–	EX?	EX?	
Anoma gracilis (C. B. Adams, 1851)	–	EX?	EX?	
Anoma integra (C.B. Adams, 1851)	–	EX?	EX?	
Anoma jarvisi Pilsbry, 1903	–	EX?	EX?	
Anoma nitens (Chitty, 1853)	–	EX?	EX?	
Anoma prunicolor (Chitty, 1853)	–	EX?	EX?	
Anoma pulchella (Chitty, 1853)	–	EX?	EX?	
Anoma pulla (Chitty, 1853)	–	EX?	EX?	
Anoma radiata (Chitty, 1853)	–	EX?	EX?	
Anoma solida (C. B. Adams, 1851)	–	EX?	EX?	
Anoma tricolor (Pfeiffer, 1847)	–	EX?	EX?	
UROCYCLIDAE				
Colparion madgei Laidlaw, 1938	EX 1994	EX	EX	
Malagarion borbonica (Morelet, 1860)	–	EX?	EX?	
Zingis radiolata Martens, 1878	CR(PE) 2004	–	EX?	
VERTIGINIDAE				
Lyropupa perlonga (Pease, 1871)	EX 1994	EX	EX	
Nesopupa turtoni (Smith, 1892)	EX 1994	EX	EX	
Vertigo bermudensis Pilsbry, 1919	–	EX?	EX?	
Vertigo marki Gulick, 1904	–	EX?	EX?	
ZONITIDAE				
Zonites embolium Fuchs and Käufel, 1936	–	EX	EX	
Zonites santoriniensis Riedel and Norris 1987	–	EX	EX	Kornilios et al., 2009
Zonites siphnicus Fuchs and Käufel 1936	–	EX	EX	Kornilios et al., 2009

Table A4. Freshwater species considered extinct (EX), possibly extinct (EX?) or extinct in the wild (EW) in the present study, compared with their status as evaluated by Régnier et al. (2009), and on the *Red List* (IUCN, 2016). *Red List* categories are extinct (EX), extinct in the wild (EW), critically endangered (possibly extinct) (CR(PE)), critically endangered (CR), least concern (LC), and data deficient (DD); the date of the IUCN evaluation follows the status. EX? is treated as equivalent to CR(PE). A dash indicates the species was not evaluated. Sources are only provided if the status in this study differs from the later of IUCN (2016) and Régner et al. (2009).

Species	*Red List*	Régnier et al., 2009	This study	Source for revised status; comments
GASTROPODA				
AMNICOLIDAE				
Amnicola rhombostoma Thompson, 1968	–	EX?	EX?	
Lyogyrus bakerianus (Pilsbry, 1917)	–	–	EX?	Johnson et al., 2013
ASSIMINEIDAE				
Pseudogibbula cara Pilsbry and Bequaert, 1927	CR(PE) 2010	–	EX?	
Valvatorbis mauritii Bequaert and Clench, 1936	CR(PE) 2010	–	EX?	
BITHYNIIDAE				
Gabbiella barthi (Brown, 1980)	CR(PE) 2016	–	EX?	
Gabbiella matadina Mandahl-Barth, 1968	CR(PE) 2010	–	EX?	
Soapitia dageti Binder, 1961	CR(PE) 2010	–	EX?	
BYTHINELLIDAE				
Bythinella eutrepha (Paladilhe, 1867)	CR(PE) 2010	–	EX?	
Bythinella gibbosa (Moquin-Tandon, 1856)	EX 2010	–	EX	
Bythinella limnopsis Letourneux and Bourguignat, 1887	EX 2010	–	EX	
Bythinella mauritanica Letourneux and Bourguignat, 1887	EX 2010	–	EX	
Bythinella microcochlia Letourneux and Bourguignat, 1887	EX 2010	–	EX	
Bythinella punica Letourneux and Bourguignat, 1887	EX 2010	–	EX	
COCHLIOPIDAE				
Dyris amazonicus (Haas, 1949)	–	EX?	EX?	
Heleobia peiranoi (Weyrauch, 1963)	–	–	EX	Rumi et al., 2006
Heleobia spinellii (Gredler, 1859)	EX 2010	–	EX	
Heleobia steindachneri (Westerlund, 1902)	–	EX	EX	
Heleobia sublineata (Pilsbry 1911)	–	–	EX	Rumi et al., 2006
Juturnia brunei (Taylor, 1987)	CR(PE) 2012	–	EX	Hershler et al., 2014
Littoridina gaudichaudii Souleyet, 1852	EX 1996	EX?	EX?	
Sioliella effusa Haas, 1949	–	EX?	EX?	
Tryonia hertleini (Drake, 1956)	–	EX	EX	
Tryonia santarosae Hershler et al., 2014	–	–	EX	Hershler et al., 2014
Tryonia shikueii Hershler et al., 2014	–	–	EX	Hershler et al., 2014
GLACIDORBIDAE				
Glacidorbis costatus Ponder and Avern, 2000	–	EX	EX	
HYDROBIIDAE				
Alzoniella galaica (Boeters and Rolan, 1988)	CR(PE) 2011	–	EX?	
Antibaria notata (Frauenfeld, 1865)	–	EX	EX	
Belgrandia moitessieri (Bourguignat, 1866)	CR(PE) 2010	–	EX?	
Belgrandia varica (Paget, 1854)	CR(PE) 2010	EX	EX?	Prié, 2010
Belgrandiella boetersi Reischütz and Falkner, 1998	CR(PE) 2010	–	EX?	
Belgrandiella cavernica Boettger, 1957	CR(PE) 2014	–	EX?	
Belgrandiella intermedia (Boeters, 1970)	EX 1996	EX	EX	
Belgrandiella kreisslorum Reischütz, 1997	CR(PE) 2010	–	EX?	
Belgrandiella multiformis Fischer and Reischütz, 1995	CR(PE) 2010	–	EX?	
Bracenica spiridoni Radoman, 1973	–	EX	EX	
Bythiospeum pfeifferi (Clessin, 1890)	–	EX?	EX?	
Dalmatinella fluviatilis Radoman, 1973	EN 2011	EX	EX	Evaluated as *Vinodolia fluviatilis* by IUCN (2016)

(*Continued*)

Table A4. (cont.)

Species	*Red List*	Régnier et al., 2009	This study	Source for revised status; comments
Dianella schlickumi Schütt, 1962	CR(PE) 2011	EX	EX?	
Falsipyrgula beysehirana (Schütt, 1965)	CR(PE) 2014	–	EX?	
Graecoanatolica brevis Radoman, 1973	CR(PE) 2014	–	EX?	Kebapçi et al., 2012
Graecoanatolica conica Radoman, 1973	CR(PE) 2014	–	EX?	Kebapçi et al., 2012
Graecoanatolica macedonica Radoman and Stanovic, 1978	EX 2002	EX	EX	
Hydrobia anatolica Schütt, 1965	CR(PE) 2014	–	EX?	
Hydrobia gracilis Morelet, 1880	EX 2010	–	EX	
Islamia ateni (Boeters, 1969)	EX 2011	–	EX	
Islamia bendidis Reischütz, 1988	CR(PE) 2011	–	EX?	
Islamia epirana (Schütt, 1962)	–	EX	EX	
Islamia graeca Radoman, 1973	CR(PE) 2011	EX	EX	
Islamia hadei (Gittenberger, 1982)	CR(PE) 2011	EX	EX	
Islamia pseudorientalica Radoman, 1973	CR(PE) 2014	–	EX?	
Kirelia carinata Radoman, 1973	CR(PE) 2014	–	EX	
Marstonia olivacea Pilsbry, 1895	EX 2000	EX	EX	
Mercuria punica (Letourneux and Bourguignat, 1887)	CR(PE) 2010	–	EX?	
Nanivitrea alcaldei (Jaume and Abbott, 1947)	–	–	EX?	Vázquez Perera and Perera Valderrama, 2010
Nanivitrea helicoides (Gundlach, 1865)	–	–	EX?	Vázquez Perera and Perera Valderrama, 2010
Neohoratia coronadoi (Bourguignat, 1870)	–	–	EX?	Arconada and Ramos, 2006
Ohridohauffenia drimica (Radoman, 1964)	EX 1994	EX	EX	
Ohridohauffenia minuta (Radoman, 1955)	CR(PE) 2010	–	EX?	
Potamopyrgus acus Haase, 2008	CR(PE) 2013	–	EX?	
Pseudamnicola barratei Letourneux and Bourguignat, 1887	EX 2010	–	EX	
Pseudamnicola doumeti Letourneux and Bourguignat, 1887	EX 2010	–	EX	
Pseudamnicola latasteana Letourneux and Bourguignat, 1887	EX 2010	–	EX	
Pseudamnicola letourneuxiana (Bourguignat, 1862)	EX 2010	–	EX	
Pseudamnicola macrostoma (Küster, 1853)	–	EX	EX	
Pseudamnicola oudrefica (Letourneux and Bourguignat, 1887)	EX 2010	–	EX	
Pseudamnicola ragia Letourneux and Bourguignat, 1887	EX 2010	–	EX	
Pseudamnicola singularis Letourneux and Bourguignat, 1887	EX 2010	–	EX	
Pseudoislamia balcanica Radoman, 1979	CR 2011	EX	EX	
Pyrgulopsis brandi (Drake, 1953)	–	EX	EX	
Pyrgulopsis carinata Hershler, 1998	–	EX	EX	
Pyrgulopsis coloradensis Hershler, 1998	–	–	EX?	Center for Biological Diversity et al., 2009
Pyrgulopsis nevadensis (Stearns, 1833)	EX 2000	EX	EX	
Pyrgulopsis ruinosa Hershler, 1998	–	EX	EX	
Pyrgulopsis torrida Hershler et al., 2016	–	–	EX?	Hershler et al., 2016
Radomaniola curta (Küster, 1853)	LC 2010	EX	EX	
Sardohoratia sulcata Manganelli et al., 1998	CR(PE) 2010	–	EX?	
Tanousia zrmanjae (Brusina, 1866)	CR(PE) 2011	EX	EX?	
Trichonia kephalovrissonia Radoman, 1973	DD 2011	EX	EX	Evaluated as *Heleobia steindachneri* by IUCN (2016)

(*Continued*)

Table A4. (cont.)

Species	*Red List*	Régnier et al., 2009	This study	Source for revised status; comments
Trichonia trichonica Radoman, 1973	CR 2011	EX	EX	
Turcorientalia hohenackeri (Küster, 1853)	VU 2011	EX	EX	
Vinodolia fiumana Radoman, 1973	EN 2014	EX	EX	
Vinodolia gluhodolica (Radoman, 1973)	EN 2010	EX	EX	
Vinodolia lacustris (Radoman, 1973)	CR 2010	–	EX	Albrecht et al., 2012
Vinodolia matjasici (Bole, 1961)	CR 2010	EX	EX	
Zaumia sanctizaumi(Radoman, 1964)	CR(PE) 2010	–	EX?	
IRIDINIDAE				
Aspatharia divaricata (Martens, 1897)	CR(PE) 2016	–	EX?	
Chambardia letourneuxi	EX 2010	–	EX	
LITHOGLYPHIDAE				
Clappia umbilicata (Walker, 1904)	EX 2000	EX	EX	
Fluminicola minutissimus Pilsbry, 1907	–	–	EX ?	Johnson et al., 2013
Fluminicola nuttallianus Lea, 1838	–	EX	EX ?	Johnson et al., 2013
Somatogyrus crassilabris Walker, 1915	EX 2000	EX	EX?	Johnson et al., 2013
Somatogyrus wheeleri Walker, 1915	EX 2000	EX	EX?	Johnson et al., 2013
LYMNAEIDAE				
Erinna aulacospira (Ancey, 1899)	DD	–	EX?	Johsnon et al., 2013
Galba cyclostoma (Walker, 1908)	–	–	EX?	Johnson et al., 2013
Galba perpolita (Dall, 1905)	–	–	EX?	Johnson et al., 2013
Galba tazewelliana (Wolf, 1870)	–	–	EX?	Johnson et al., 2013
Galba vancouverensis (F.C. Baker, 1939)	–	–	EX?	Johnson et al., 2013
Lantzia carinata (Jousseaume, 1872)	CR(PE) 2016	–	EX?	
Lymnaea plicata Hylton Scott 1953	–	–	EX	Rumi et al., 2006
Stagnicola neopalustris (F.C. Baker, 1911)	–	–	EX?	Johnson et al., 2013
Stagnicola petoskeyensis (Walker, 1908)	–	–	EX?	Johnson et al., 2013
Stagnicola pilsbryi Hemphill, 1890	EX 2012	EX	EX	
Stagnicola utahensis (Call, 1884)	CR(PE) 2012	–	EX	Center for Biological Diversity et al., 2009
MELANOPSIDAE				
Melanopsis germaini Pallary, 1939	CR(PE) 2014	–	EX?	
Melanopsis infracincta Martens, 1874	CR(PE) 2014	–	EX?	
Melanopsis khabourensis Pallary, 1939	CR(PE) 2014	–	EX?	
Melanopsis pachya Pallary, 1939	CR(PE) 2014	–	EX?	
Melanopsis parreyssii (Philippi, 1847)	CR 2011	–	EX	Sîrbu and Benedek, 2016
MOITESSIERIIDAE				
Henrigirardia wienini (Girardi, 2001)	CR(PE) 2010	–	EX?	
Iglica gratulabunda (Wagner, 1910)	CR(PE) 2010	–	EX?	
Paladilhiopsis janinensis Schütt, 1962	CR(PE) 2011	EX	EX?	
Spiralix corsica Bernasconi, 1994	CR(PE) 2010	–	EX?	
NERITIDAE				
Neritina tiassalensis Binder, 1955	CR(PE) 2010	–	EX?	
PACHYCHILIDAE				
Sulcospira martini (Schepmann, 1898)	–	EX?	EX?	
Sulcospira pisum (Brot, 1868)	–	–	EX?	Marwoto and Isnaningsih, 2012
Sulcospira sulcospira (Mousson, 1849)	DD 2011	EX?	EX?	Marwoto and Isnaningsih, 2012
PHYSIDAE				
Physella microstriata (Chamberlain and Berry, 1930)	EX 2000	EX	EX	
PLANORBIDAE				
Amphigyra alabamensis Pilsbry, 1906	EX 2000	EX	EX	
Ceratophallus concavus (Mandahl-Barth, 1954)	CR(PE) 2016	–	EX ?	
Glyptophysa oconnori (Cumber, 1941)	DD 2011	–	EX	Spencer et al., 2009
Neoplanorbis carinatus Walker, 1908	EX 2000	EX	EX	
Neoplanorbis smithi Walker, 1908	EX 2000	EX	EX	
Neoplanorbis tantillus Pilsbry, 1906	EX 2012	EX	EX	
Neoplanorbis umbilicatus Walker, 1908	EX 2000	EX	EX	

(*Continued*)

Table A4. (cont.)

Species	*Red List*	Régnier et al., 2009	This study	Source for revised status; comments
Planorbella columbiensis (F.C. Baker, 1935)	–	–	EX?	Johnson et al., 2013
Planorbella multivolvis (Case, 1847)	EX 2000	EX	EX	
Planorbella traskii (Lea, 1856)	–	–	EX	Johnson et al., 2013
Rhodacmea hinkleyi (Walker, 1908)	–	–	EX?	Johnson et al., 2013
Vorticifex solida (Dall, 1870)	–	–	EX?	Johnson et al., 2013
PLEUROCERIDAE				
Athearnia crassa (Haldeman, 1841)	EX 1996	EX	EX	
Elimia brevis (Reeve, 1860)	EX 2000	EX	EX	
Elimia clausa (Lea, 1861)	EX 2000	EX	EX	
Elimia fusiformis (Lea, 1861)	EX 2000	EX	EX	
Elimia gibbera (Goodrich, 1922)	EX 2000	EX	EX	
Elimia hartmaniana (Lea, 1861)	EX 1994	EX	EX	
Elimia impressa (Lea, 1841)	EX 1994	EX	EX	
Elimia jonesi (Goodrich, 1936)	EX 1994	EX	EX	
Elimia laeta (Jay, 1839)	EX 1994	EX	EX	
Elimia macglameriana (Goodrich, 1936)	EX 2000	EX	EX	
Elimia pilsbryi (Goodrich, 1927)	EX 1994	EX	EX	
Elimia pupaeformis (Lea, 1864)	EX 1994	EX	EX	
Elimia pupoidea (Anthony, 1854)	–	–	EX	Johnson et al., 2013
Elimia pygmaea (Smith, 1936)	EX 1994	EX	EX	
Gyrotoma excisa (Lea, 1843)	EX 2000	EX	EX	
Gyrotoma lewisii (Lea, 1869)	EX 2000	EX	EX	
Gyrotoma pagoda (Lea, 1845)	EX 2000	EX	EX	
Gyrotoma pumila (Lea, 1860)	EX 2000	EX	EX	
Gyrotoma pyramidata (Shuttleworth, 1845)	EX 2000	EX	EX	
Gyrotoma walkeri (Smith, 1924)	EX 2000	EX	EX	
Leptoxis clipeata (Smith, 1922)	EX 2000	–	EX	
Leptoxis formosa (Lea, 1860)	EX 2000	EX	EX	
Leptoxis ligata (Anthony, 1860)	EX 2000	EX	EX	
Leptoxis lirata (Smith, 1922)	EX 2000	EX	EX	
Leptoxis minor (Hinkley, 1912)	–	–	EX	Johnson et al., 2013
Leptoxis occultata (Smith, 1922)	EX 2000	EX	EX	
Leptoxis showalterii (Lea, 1860)	EX 2000	EX	EX	
Leptoxis torrefacta (Goodrich, 1922)	EX 2000	EX	EX	
Leptoxis trilineata (Say, 1829)	–	–	EX	Johnson et al., 2013
Leptoxis vittata (Lea, 1860)	EX 2000	EX	EX	
Lithasia hubrechti Clench, 1956	–	–	EX	Johnson et al., 2013
Lithasia jayana (Lea, 1841)	–	–	EX	Johnson et al., 2013
POMATIOPSIDAE				
Pomatiopsis hinkleyi Pilsbry, 1896	–	–	EX?	Johnson et al., 2013
TATEIDAE				
Beddomeia tumida Petterd, 1889	CR(PE) 2011	EX	EX?	Clark, 2011
Fluvidona dulvertonensis (Tennison-Woods, 1876).	EX 1996	EX	EX	
Leiorhagium solemi Haase and Bouchet, 1998	EX 2011	EX?	EX?	
Posticobia norfolkensis (Sykes, 1900)	EX 1996	EX	EX	
Potamolithus concordianus Parodiz, 1966	–	–	EX	Rumi et al., 2006
THIARIDAE				
Aylacostoma brunneum Vogler and Peso, 2014	–	–	EW	M.G. Quintana, pers. comm., 2016
Aylacostoma chloroticum Hylton-Scott, 1953	EW 2000	EW	EW	M.G. Quintana pers. comm., 2016
Aylacostoma guaraniticum Hylton-Scott, 1953	EW 2000	EW	EX	Rumi et al., 2006; M.G. Quintana pers. comm., 2016
Aylacostoma stigmaticum Hylton-Scott, 1953	EW 2000	EW	EX	Rumi et al., 2006; M.G. Quintana pers. comm., 2016

(*Continued*)

Table A4. (cont.)

Species	*Red List*	Régnier et al., 2009	This study	Source for revised status; comments
Melanoides agglutinans (Bequaert and Clench, 1941)	CR(PE) 2010	–	EX?	
VALVATIDAE				
Valvata klemmi Schütt, 1962	EN 2011	EX	EX	
Valvata virens Tryon, 1863	–	–	EX?	Johnson et al., 2013
VIVIPARIDAE				
Bellamya phthinotropis (Martens, 1892)	CR(PE) 2016	–	EX?	
Viviparus bermondianus (d'Orbigny, 1842)	–	EX	EX	
BIVALVIA				
CORBICULIDAE				
Corbicula linduensis Bollinger, 1914	–	EX?	EX?	
Corbicula subplanata Martens, 1897	–	EX?	EX?	
DREISSENIDAE				
Dreissena caspia Eichwald, 1855	CR(PE) 2011	–	EX?	
MYCETOPODIDAE				
Anodontites moricandi (Lea, 1860)	–	EX?	EX?	
SPHAERIIDAE				
Eupera crassa (Mandahl-Barth, 1954)	CR(PE) 2016	–	EX?	
Pisidium betafoense Kuiper, 1953	CR(PE) 2016	–	EX?	
UNIONIDAE				
Alasmidonta mccordi Athearn, 1964	EX 2000	EX	EX	
Alasmidonta robusta Clarke, 1981	EX 2000	EX	EX	
Alasmidonta wrightiana (Walker, 1901)	EX 2000	EX	EX	
Coelatura rothschildi (Neuville and Anthony, 1906)	CR(PE) 2016	–	EX?	
Cuneopsis demangei Haas, 1929	CR(PE) 2011	–	EX?	
Elliptio nigella (Lea, 1852)	CR 2012	EX	EX	
Epioblasma arcaeformis (Lea, 1831)	EX 2000	EX	EX	
Epioblasma biemarginata (Lea, 1857)	EX 2000	EX	EX	
Epioblasma flexuosa (Rafinesque, 1820)	EX 2000	EX	EX	
Epioblasma haysiana (Lea, 1834)	EX 2000	EX	EX	
Epioblasma lenior (Lea, 1842)	EX 2000	EX	EX	
Epioblasma lewisii (Walker, 1910	EX 2000	EX	EX	
Epioblasma othcaloogensis (Lea, 1857)	CR(PE) 2012	–	EX?	
Epioblasma personata (Say, 1829)	EX 2000	EX	EX	
Epioblasma propinqua (Lea, 1857)	EX 2000	EX	EX	
Epioblasma sampsonii (Lea, 1862)	EX 2000	EX	EX	
Epioblasma stewardsonii (Lea, 1852)	EX 2000	EX	EX	
Epioblasma turgidula (Lea, 1858)	EX 2000	EX	EX	
Germainaia geayi (Germain, 1911)	EX 2016	–	EX	
Lamprotula crassa (Wood, 1815)	CR(PE) 2011	–	EX?	
Lamprotula liedtkei Rolle, 1904	CR(PE) 2011	–	EX?	
Lamprotula nodulosa (Wood, 1815)	CR(PE) 2011	–	EX?	
Lampsilis binominata Simpson, 1900	EX 2000	EX	EX	
Medionidus mcglameriae van der Schalie, 1939	EX 2000	EX	EX	
Obovaria haddletoni (Athearn, 1964)	CR(PE) 2012	–	EX?	
Pleurobema altum (Conrad, 1854)	EX 2000	EX	EX	
Pleurobema avellanum Simpson, 1900	EX 2000	EX	EX	
Pleurobema bournianum (Lea, 1840)	EX 2000	EX	EX	
Pleurobema chattanoogaense (Lea, 1858)	–	EX	EX	
Pleurobema curtum Lea, 1859	CR(PE) 2012	–	EX?	
Pleurobema flavidulum (Lea, 1861)	EX 2000	–	EX	
Pleurobema hagleri Frierson, 1900	EX 2000	–	EX	
Pleurobema hanleyianum (Lea, 1852)	CR 2012	EX	EX	
Pleurobema johannis (Lea, 1859)	EX 2000	–	EX	
Pleurobema murrayense (Lea, 1868)	EX 2000	–	EX	
Pleurobema nucleopsis (Conrad, 1849)	EX 2000	–	EX	

(*Continued*)

Table A4. (cont.)

Species	*Red List*	Régnier et al., 2009	This study	Source for revised status; comments
Pleurobema perovatum (Conrad, 1834)	EX 2000	–	EX	
Pleurobema troschelianum (Lea, 1852)	EX 2000	–	EX	
Pleurobema verum (Lea, 1861)	EX 2000	EX	EX	
Quadrula tuberosa (Lea, 1840)	CR 1996	EX	EX	Evaluated as *Theliderma tuberosa* by IUCN (2016)

Table A5. Marine species considered extinct (EX) or possibly extinct (EX?) in the present study, compared with their status as evaluated by Régnier et al. (2009), and on the *Red List* (IUCN, 2016). Dashes indicate that the species was not evaluated. A source is only provided for species of Conidae, for which the status in this study differs from that of IUCN (2016) and Régner et al. (2009).

Species	*Red List*	Régnier et al., 2009	This study	Source for revised status
CONIDAE				
Conasprella sauros (Garcia, 2006)	DD	–	EX?	Peters et al., 2013
Conus bellulus Rolán, 1990	–	–	EX?	Peters et al., 2013
Conus colmani Röckel and Korn, 1990	DD	–	EX?	Singleton, 2007
LOTTIIDAE				
Lottia alveus Conrad, 1831	EX 1994	EX	EX	
NACELLIDAE				
Collisella edmitchelli Lipps, 1966	EX 1996	EX	EX	
POTAMIDIDAE				
Cerithideopsis fuscata (Gould, 1857)	–	EX	EX	

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Is mining the seabed bad for mollusks?

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ABSTRACT

Up to three miles below the ocean surface, deep-sea hydrothermal vents are home to a community of extraordinary mollusks. In an environment without light, under intense pressure and volcanic heat, many gastropods and bivalves living directly on the vent chimneys show adaptations that have driven important scientific breakthroughs. For example, the famous "scaly-foot" gastropod, *Chrysomallon squamiferum*, has hard scales on its foot with a crystalline iron coating that has inspired novel defensive armor designs. This iconic species has only been reported from three sites in the Indian Ocean, each site hundreds of miles apart and only around half the size of a football field. Two of these three sites are already designated under international exploration licenses for deep-sea mining, to extract rare minerals from the vent chimneys. Economic and political pressures to exploit the seabed are advancing much faster than scientific exploration, putting these vent ecosystems and their molluscan residents at risk.

MOLLUSKS IN THE DEEP SEA

General perception of marine mollusks is naturally driven by our access to shallow marine species commonly found on beaches and the history of shell collecting. The species and varied ecosystems found in the deep sea are less familiar to non-specialists.

The deep oceans represent a broad variety of habitats and ecosystems, distributed across a three-dimensional volume of water that represents over 90% of the habitable space on Earth (Costello et al., 2010; Rex and Etter, 2010). Mollusks inhabiting the ocean floor cover its entire range, from shallow coastal environments to the deep sea. The characteristics of the deep sea vary geographically, for example the depths of thermoclines, insolation, and lysoclines (depth of carbonate saturation), vary latitudinally and between ocean basins (Rex et al. 2000; Steele et al. 2009). These physical and chemical conditions represent specific challenges or adaptive pressures, which manifest in shell forms that are distinctly different than shallow-water species more commonly seen in shell collections: aphotic conditions below 1000 m or less result in a lack of shell pigmentation (Abbott, 1985), and calcium limitation at depths below 3000–4000 m (Morse et al., 2007) results in typically thin and fragile shells. Aesthetics combined with the expense and technical challenges of deep-sea exploration mean that the shells of deep-sea species are, unusually for mollusks, not generally available on the commercial market.

Access to study deep-sea habitats principally depends on large-scale ocean going research vessels equipped with specialized sampling equipment. Such infrastructure is generally only available through support from government funding of major nations, and indeed most deep-sea exploration focuses on geology, oceanography, climate change, and many other aspects besides sampling benthic animals such as mollusks. The large-scale investment and funding required, and the rarity of these samples, ethically demand that all such materials should be held permanently in public collections and preserved for further research and education.

The ocean floor remains largely unexplored: perhaps 10% of the seafloor has been mapped by ship-borne instrumentation and far less has been sampled biologically (Charette and Smith, 2010). Ongoing sampling of deep-sea communities continues to uncover new species, even in areas that are relatively well studied like the NW Atlantic (Grassle and Maciolek, 1992). However, the deep-sea is biologically nutrient-limited, and many species appear to live in very low densities. So deep-sea species may rely on strong dispersal mechanisms to find sufficient habitat and thus have generally larger ranges than shallow water species both in terms of depth range and geographic range (Costello et al., 2011). The primary data for this pattern comes from fish rather than benthic invertebrates, therefore it may not be valid to infer a global generalization. Indeed, patterns in bathymetric

ranges in the pelagic realm are very similar to latitudinal ranges of terrestrial groups (Brown et al., 1996). Deep-sea benthic habitats are heterogeneous and represent landscapes that vary on scales of hundreds of kilometers (Levin et al., 2001), which is not dissimilar to the magnitude of some continents. As a result, how many deep-sea species are endemic to the specific area where they were discovered, or simply have only been found there because of poor sampling, remains highly debated.

Apart from this overall diversity on the undersea mountains, valleys, and plains, there are oases that host astonishing high-density biomass in chemoautotrophic-based ecosystems. Geothermal energy is the foundation for hydrocarbon "cold" seeps and hydrothermal vents, or direct nutrient input can come from organic falls (such as whale carcasses and wood). All represent high-quality energy input to the deep-sea ecosystem constrained at a very small spatial scale (Gage and Tyler, 1992).

Food chains building on chemoautotrophic microbes form a suite of specialist animal species that is unique to each type of ecosystem. Specialist vent endemic species cannot live in other deep-sea sites such as whale falls (Wolff, 2005), and there is little overlap in vent and seep fauna. There are some ecological similarities among these "oases", and some larger evolutionary radiations such as bathymodioline mussels or lepidopleuran chitons include species that colonize different deep-sea habitats (Thubaut et al., 2013; Sigwart, 2016), but each species is restricted to its own specialism.

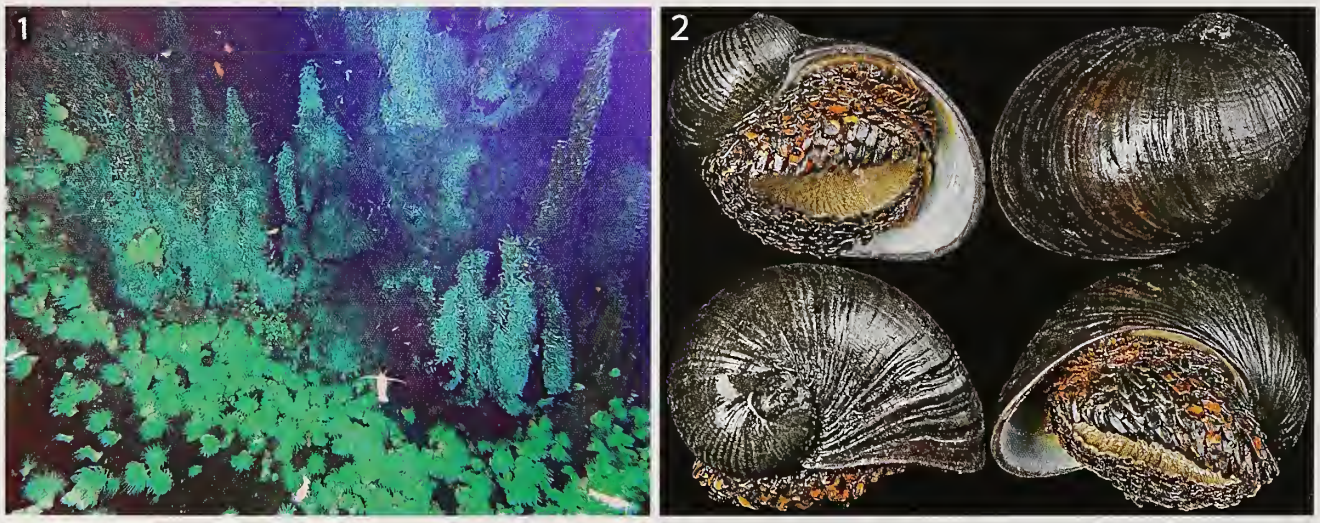
At hydrothermal vents, seawater circulating through the seafloor is heated and enriched with reduced compounds; when the fluids emerge back into the main ocean, minerals precipitate around the fluid flow, often creating characteristic chimneys or "black smokers". Images of these habitats show the vertical walls of the chimneys teaming with life (Figure 1), and the vent ecosystems are dominated by relatively few species occurring in very high biomass, comparable to the density of life supported by tropical coral reefs (Van Dover, 2000).

The gastropods living in vent ecosystems include a large number of endemic lineages (McArthur and Tunnicliffe 1998), including unusual recently-derived adaptations such as the "scaly-foot" gastropod (*Chrysomallon squamiferum* Chen et al., 2015) in the Indian Ocean (Chen et al., 2015a). Each mollusk species lives in a "Goldilocks zone" (not too hot and not too cold) with very narrowly defined limits of temperature and ocean chemistry, somewhere on the gradient where mineral-rich superheated vent fluid emerges at over 300°C and is rapidly cooled by surrounding seawater at around 2°C. Species' varying tolerances for temperature and acidic vent fluid create patches or zones dominated by particular taxa, much like the zonation in rocky intertidal shores (Van Dover, 2000).

Hydrothermal vents were first discovered in 1977 (Lonsdale, 1977; Van Dover, 2000). The identification of these self-contained ecosystems at 2550 m depth on the Galápagos Rift was a sea change for biology. Much of our knowledge about vent systems in general, is based on generalizations predicted from these earliest-discovered and best-understood sites. Since then, other vent sites, hosting different specialist communities, have been discovered in every ocean and more remain to be found (Rogers et al., 2012). Vents are known to occur at all actively spreading ocean ridges, back-arc basins, and some seamounts. Here we consider the impact of the advance of knowledge about deep sea ecosystems on our understanding of molluscan biodiversity and its conservation.

HYDROTHERMAL VENTS, FAST AND SLOW

The tectonic geology of the seabed is different, in different ridge systems around the globe. There are at least



Figures 1–2. The Kairei Vent Field, Central Indian Ridge. **1.** Overview of the Monju site in the Kairei Vent Field, the foreground is covered by anemones, the spires of chimneys are covered by dense aggregations of vent shrimp (one seen swimming in foreground). **2.** *Chrysomallon squamiferum* from the Kairei Vent Field, shell length = 39.1 mm.

11 distinct biogeographic provinces among vent systems along the mid-ocean ridges and back-arc spreading centers of the global seafloor (Rogers et al., 2012). The distribution of animals among these widely separated habitats is largely explained by the local sea-floor spreading rates (Tunnicliffe and Fowler, 1996). Fast-spreading centers such as East Pacific Rise (EPR) have rapidly forming black smoker chimneys that are prone to collapse and re-grow on sub-decadal timescales (Shank et al., 1998); slow spreading centers, such as the Southwest Indian Ridge, may have physical vent structures and communities that are stable over multi-decadal or even much longer timescales (Lalou et al., 1990). Vent fields that are close to each other, on a scale of hundreds of kilometers apart, have similar but often non-identical species assemblages (Van Dover, 2001) whereas vent systems on different ocean ridges represent entirely different faunas (Ramirez-Llodra et al., 2007; Rogers et al., 2012).

The majority of detailed studies come from EPR and the mid-Atlantic ridge, which are distinctly different from all other global vent fields in terms of their fauna, biogeography, dispersal potential, and spreading rates of the underlying geology (Van Dover et al. 2002). The first exploration of vent fields in the Indian Ocean showed relatively minor differences in underlying geology compared predicted patterns, but dramatically different fauna (Van Dover, 2001).

Despite these clear differences, the uniquely fast turnover of the EPR fauna seems to be the basis of generalizations about hydrothermal vent ecosystems. Other vent systems, with slower turnover, are inevitably more sensitive to and much slower to recover from any disturbance.

Conservation of the deep sea, including hydrothermal vents, must account for the modern understanding of geographical variation in ecosystems. Hydrothermal vents occur even at the slowest spreading portions of global mid-ocean ridges such as the Southwest Indian Ridge and the Arctic Ocean (Tivey, 2004; Pederson, et al., 2010). Slower spreading seems to correlate with more stable faunal communities, low natural disturbance, and probably higher sensitivity and slower recovery from disturbance (Van Dover, 2014); however, these same slow-spreading centers may also generate comparatively large mineral deposits (Tao et al., 2014). Thus the most sensitive areas are the primary target for commercial exploitation. And the assessment of the potential damage of that exploitation is inferred from a dissimilar system.

Individual vent fields vary in scale but tend to be at most a few kilometers across. Images of dense biomass can be misleading, as the surrounding context of empty ocean is never visible. Some iconic vent sites are actually tiny; the Kairei Vent Field on the Central Indian Ridge, where the scaly-foot gastropod was first discovered, covers an area 80×30 m, less than half the size of a football field (Van Dover, 2001). Contrast this to feasibility studies, which have shown that current demand for rare earth minerals for only one year's global consumption requires extraction of 5 km^2 of seabed (Kato et al., 2013). That represents mining activity over more than 2000 times the size of the entire Kairei Vent Field, every year.

It is unclear whether the value of the minerals extracted could ever offset the extreme cost and risk of deploying mining equipment to the deep sea, and the environmental damage caused to the seabed.

DEEP-SEA MINING

The United Nations (1994a) Convention on the Law of the Sea (UNCLOS) laid boundaries for the control of coastal access and coastal resources. Territorial waters of each nation extend only 12 nautical miles (22.2 km) from the low-water mark of its coastline, and the Exclusive Economic Zone (EEZ) extends beyond that to a further distance of up to 200 nautical miles (370.4 km). Within this region (and some additional distance where the continental shelf extends beyond the 200 nautical miles limit), each country holds control of the seabed and the pelagic realm for mining, fishing, and other activities. Beyond that limit, the great majority of the area and volume of the Earth's oceans, are "international waters", the high seas, *mare liberum*: belonging to no-one and everyone. All states have equal freedom of passage, fishing, and access for research in international waters.

The legal control of the oceans is defined by distance from land, not by depth. What constitutes "deep" sea is not strictly defined, and the physical properties of seawater at depth (solar penetration, temperature, oxygen, current speeds) vary in different parts of the globe, but a minimum of 1000 m is generally accepted as biologically "deep" (Gage and Tyler, 1992). Coastal shells that are familiar in commercial trade come from near shore—even collectible species that are colloquially referred to as "deep water" are almost all captured within the exclusive economic zone of the country of origin. For example, many species and forms of *Zoila* spp. from Australia are sold as "deep water" cowries, but live mainly within the limits of deep human diving, to a maximum depth of perhaps 300 m (Lorenz and Hubert, 2002). Most people think of *Nautilus* spp. as "deep-sea shells", yet their shells actually implode at depths of around 750–900 m (Kanie and Hattori, 1983; Vermeij, 1993). The family Pleurotomariidae or "slit shells" is famous as a group of generally rare and collectible "deep-sea" gastropods, but their bathymetric range only extends to a maximum just shy of 1000 m (Harasewych, 2002).

We may think of the high seas as inaccessible, and not available for commercial exploitation, apart from the rather transient activities of shipping and fishing. The seafloor of the "free seas" may seem both practically and financially remote, and under the implicit protection of the United Nations. In implementing the Convention on the Law of the Sea (United Nations, 1994a), the United

Nations (1994b) established the International Seabed Authority (ISA) exactly to administer access to the floor of the ocean beyond states' jurisdiction (Jaeckel, 2015). The text of the original UN resolution includes the statement that it was:

> "Reaffirming that the seabed and ocean floor ... are the common heritage of mankind, Mindful of the importance of the Convention for the protection and preservation of the marine environment and of the growing concern for the global environment ..." (United Nations, 1994b: 3)

In July 2016, the ISA published a full working draft of exploitation regulations to govern the active extraction of minerals from mining the seabed in the high seas (ISA 2016). Exploration for commercial deep-sea mining is already well underway. The first set of 15-year licenses for mining exploration issued by the ISA to governments and commercial mining interests have already expired. Exploration licenses were granted to seven different groups from Europe, Russia, Korea, China, Japan, and India, with contracts starting in 2001–2002, and all have applied for contract extensions. The challenge for the ISA is to balance commercial pressures with a mandate to manage conservation, in a data limited environment and a largely untested legal framework (Jaeckel, 2016).

The reality of deep-sea mining, including heavy machinery deployed to the abyss, seems to stand in stark contrast to the unexplored inaccessible mysteries of the deep. But the technology is rapidly advancing, driven by potential access to valuable rare minerals, and international competition for first access to a new commercial frontier (Hoagland et al., 2010; Aldhous, 2011). The key targets of seabed exploitation are polymetallic nodules, polymetallic sulfides, and cobalt-rich ferromanganese crusts. Sulfides, rare earth minerals, and rare metals, including cobalt, are found in high densities at sites of geological spreading activity, such as hydrothermal vents (Tao et al., 2014; Van Dover, 2014).

The vivid images of dense communities and biomass at hydrothermal vents, in an ecosystem with no sunlight, are now a familiar part of deep-sea biology. The geological setting of vents creates habitat, small oases in the deep sea dependent on geothermal energy, but also exploitable concentrations of mineral deposits. Thus, vent areas globally became focal points for both conservation concerns and commercial exploitation. This conflict has been dismissed in many studies, based on misunderstanding of the diversity of vent geology and vent biota.

OUT OF SIGHT, BUT NOT OUT OF MIND

There are important reasons that prevent deep-sea mollusks from direct commercial exploitation for the shell collecting trade. Publicly funded scientific expeditions are currently the only mechanism for collecting these shells in most localities. To ensure the protection, preservation, and inclusive scientific access to this precious material, they belong in permanent, publicly available museum collections, not in the control of individual researchers or private citizens. Public education about these animals is also crucial to their future survival. A disconnect between scientists and mollusk enthusiasts may be to the detriment of conservation efforts.

We consider the scaly-foot gastropod, *Chrysomallon squamiferum* (Chen et al., 2015a: Figure 2), as a case study of an animal that is popular and well-known, but that lacks protection or detailed study in its own hydrothermal vent habitat. The scaly-foot gastropod is an iconic member of the Indian Ocean hydrothermal vent fauna, known for the mineralized scales that cover the outer surface of its foot (Chen et al., 2015b). This species has been reported from only three sites since its discovery in 2000. Its total habitat covers less than 0.02 km^2 or less than one-fifth of a football field in total range, spread over an area of nearly 1,000,000 km^2 (925,347 km^2) (Figure 3).

Among the three sites where the scaly-foot has been reported, two are located in Area's Beyond National Jurisdiction (ABNJ) and therefore fall under the legal mandate of the ISA. The Solitaire Vent Field occupies an area of 50×50 m and is within the EEZ of Mauritius (Nakamura et al., 2012). The Kairei Vent Field is of very similar size, at around 30×80 m (Van Dover et al., 2001), but 773 km south of Solitaire, the entire area of Kairei Vent Field is under an active mining exploration license granted to Germany (2015–2030) by the ISA. The third, southernmost reported population is located 2563 km to the southwest, at Longqi Vent Field. There, the main vent field spans 100×150 m (Tao et al., 2014), and this and the surrounding areas are under a mining exploration license granted to China (2011–2026). The conservation status of this species has not yet been assessed by the IUCN, although a population genetic study examining the connectivity among the three populations revealed poor connectivity between Longqi and the other two populations, implying dispersal barrier exist across the two ridges (Chen et al., 2015c). There are no conservation measures in place, and none have yet been proposed, for any of these sites.

Each hydrothermal vent site, especially those in the remote Indian Ocean, are observed on average less than once a year by the collective global endeavor of scientists, and independent monitoring of any commercial activity in such sites is nearly impossible. There is a small island in the River Thames, UK, designated as a nature reserve to protect terrestrial snails and other wildlife (Burns et al., 2013). At 9 acres (0.035 km^2), Isleworth Ait is almost twice the area of the entire known habitat for *Chrysomallon squamiferum*, and this island is not the only reserve for the two-lipped door snail *Alinda biplicata* (Montagu, 1803). Additional protection for deep-sea biota would seem to be warranted.

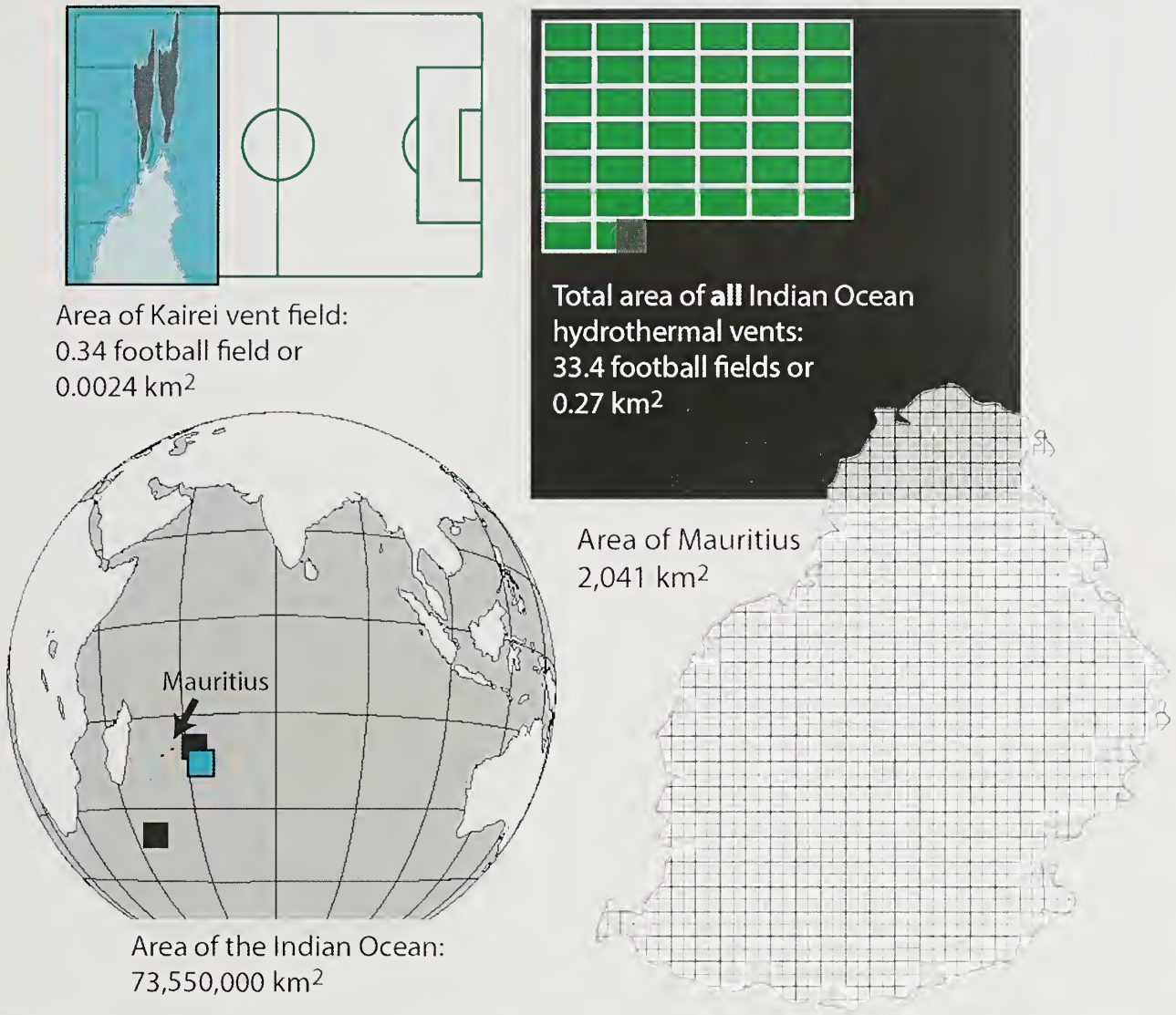


Figure 3. Infographic depicting the relative scale of hydrothermal vent sites. Top left, the area of Kairei Vent Field on the Central Indian Ridge is shown as the blue box relative to a sports field conforming to regulations of Fédération Internationale de Football Association (FIFA), 105×70 m. Top right, the sum of all Indian Ocean hydrothermal vent fields, represented to scale in green playing fields, against an 1 km^2 black square. This area was calculated based on a count of 37 reported Indian Ocean sites of vent activity according to the InterRidge international database, and an arithmetic average size of 7225 m^2 per vent field, based on the four well-mapped confirmed active sites (Edmond, Kairei, Solitaire, Longqi). The island of Mauritius is shown with approximately 1-km grid squares. At bottom left, the map of the Indian Ocean compares the location of Mauritius and the three vent sites where the scaly-foot gastropod, *Chrysomallon squamiferum*, has been found (Solitaire, Kairei in blue, and Longqi; boxes not to scale).

There are more than 712 animal species described from hydrothermal vents, in only 40 years since the first dramatic discovery of these ecosystems (Wolff, 2005). Among these are more than 250 mollusk species and that number is continuously increasing. Study of hydrothermal vents changed thinking about the limits of life on earth, expanding to a world without solar energy (Van Dover, 2000). This has expanded scientific knowledge but also enriched the understanding of our planet for everyone. Scientists and citizens alike have a role to voice concern over potentially permanent damage to the deep oceans.

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End of the *Mollusks in Peril 2016 Forum* Section

Taxonomic reexamination of three vesicomyid species (Bivalvia) from the middle Miocene Bessho Formation in Nagano Prefecture, central Japan, with notes on vesicomyid diversity

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ABSTRACT

The middle Miocene Bessho Formation in central Japan consists of siltstone deposited on the slope of a back-arc basin, and contains cold-seep carbonate bodies of various sizes. We describe four vesicomyid species from this formation, one of them new, *Pliocardia? tanakai* new species, one in open nomenclature, *Adulomya* sp. 1, and two previously reported species, *Adulomya uchimuraensis* Kuroda, 1931 and *Calyptogena akanudaensis* Tanaka, 1959, the latter here reassigned to the genus *Adulomya*. The relative abundances of the four vesicomyid species are different among fossil localities, apparently related to size, lithology, and the carbon isotopic signature of the carbonate bodies. First, large carbonate mounds composed of micrite and calcite veins, with $\delta^{13}C$ values of −40 to −36‰ vs. PDB, are dominated by *A. uchimuraensis*, with *A. akanudaensis* and *Pliocardia? tanakai* new species being minor constituents. Second, siltstone containing cm-sized carbonate concretions with $\delta^{13}C$ values as low as −35‰ contains only rare and scattered specimens of *Adulomya* sp. 1. Third, at a carbonate body, ~1 m in diameter and composed mainly of micrite with $\delta^{13}C$ values of −29.8 to +10.5‰, *A. akanudaensis* and *A. uchimuraensis* are about equally abundant. These distribution patterns suggest that the vesicomyid species diversity in the Bessho Formation might have been related to variations in the physico-chemical characteristics of the seep environment, such as fluid flux rates and/or seep longevity.

Additional Keywords: Pliocardia, new species, *Adulomya*, Vesicomyidae, middle Miocene, cold seeps

INTRODUCTION

Vesicomyid bivalves first appeared at the middle Eocene cold-seep sites in North Pacific, and they are now dominant animals in various deep-sea reducing environments such as cold seeps, hydrothermal vents, and whale falls all over the world (Amano and Kiel, 2007; Taylor and Glover, 2010; Krylova and Sahling, 2010). The family Vesicomyidae is one of the most species-rich families among chemosynthesis-based animals, with more than 100 species described so far (Decker et al., 2012). A recent molecular phylogenetic analysis of the vesicomyids by Decker et al. (2012) suggested recurrent events of "stepwise speciation" from shallow to deep waters in different ocean basins, which is consistent with bathymetric segregation among the extant genera and species (Fujikura et al., 2000; Cosel and Olu, 2009; Krylova and Sahling, 2010). For more discussion on vesicomyid species diversity we should also pay attention to co-occurrences of two or more species from the same area, both in modern (e.g., Callender and Powell, 1992; Barry et al., 1997; Kojima and Ohta, 1997; Krylova and Janssen, 2006; Fujikura et al., 2008) and ancient seep sites (Tanaka, 1959; Amano et al., 2010; Kiel, 2010; Kiel and Amano, 2010; Amano and Kiel, 2012).

The middle Miocene Bessho Formation in Nagano Prefecture, central Japan, hosts cold-seep carbonate bodies of various sizes, some of which yield two or more vesicomyid species (Koike and Miyajima, 2016). The large seep carbonate bodies at Akanuda and Anazawa have been reported to yield two vesicomyid species, *Adulomya uchimuraensis* Kuroda, 1931, and *Calyptogena akanudaensis* Tanaka, 1959 (Tanaka, 1959; Kanno et al., 1998). *Adulomya uchimuraensis* has been studied and revised by Kanno et al. (1998) and Amano and Kiel (2011), but *C. akanudaensis* was beyond the scope of these studies and its generic assignment was postponed, because its internal characters were unknown.

This paper focuses on taxonomical reexamination on vesicomyid species from the Bessho Formation. We reassign *Calyptogena akanudaensis* to the genus *Adulomya* Kuroda, 1931, on the basis of its internal shell characters recognized in type materials and our newly collected fossil specimens. We also newly describe *Pliocardia? tanakai* new species and report another species, *Adulomya* sp. 1, in open nomenclature. Habitat preferences of the four species are discussed based on their relative abundance,

mode of occurrences, and the petrographic and geochemical characteristics of the hosting seep carbonates.

MATERIALS AND METHODS

The Bessho Formation is mainly composed of dark-gray siltstone deposited at a back-arc basin after the opening of the Japan Sea (Harayama, 2006). The examined vesicomyid fossils are from three localities in the northern part of Matsumoto City, i.e., Akanuda and Anazawa (Loc. 1), Sorimachi (Loc. 2), and Tonohara (Loc. 3), as shown in Figure 1. Kato et al. (2011) estimated the sedimentary environment of the Bessho Formation to be upper- to upper middle-bathyal depths under warm current, based on a benthic foraminiferal assemblage from Loc. 1 and other fossil occurrences (Kosaka and Taguchi, 1983; Noda et al., 1986; Itoigawa and Yanagisawa, 2002). Kato et al. (2011) assigned the planktonic foraminiferal and calcareous nannofossil assemblages from Loc. 1 to the PF2/PF3 zones of Maiya (1978) and the CN5a zone of Okada and Burkry (1980), corresponding to an absolute age of 13.6 to 13.1 Ma, according to Saito (1999).

We reexamined vesicomyid fossil specimens in the collection of Kunio Tanaka (Emeritus Professor of Shinshu University, Japan) from seep carbonate bodies at Akanuda and Tonohara (Locs. 1 and 3), which are deposited in the Shinshushinmachi Fossil Museum (SFMKT-00144, 00389, 00398, 00399, 00401–00407, and 07227–07230). In addition, abundant vesicomyid fossil specimens collected by us from the three localities were also examined. The specimens were carefully cleaned using an air scribe and needles to expose hinge characters, measured to the nearest 0.1 mm using a caliper, and photographed with ammonium chloride coating. All specimens are deposited in the Shinshushinmachi Fossil Museum (SFM) and the Department of Geology and Mineralogy, Kyoto University, Japan (KUG).

We analyzed carbon stable isotopic compositions of the carbonates from localities 2 and 3, in order to examine whether or not they were related to methane seepage. Powdered samples, taken from cut slabs using a microdrill, were reacted with 100% orthophosphoric acid in vacuum at 90 °C for 1000 s, and analyzed in a mass spectrometer IsoPrime 100 (Isoprime) at the Department of Geology and Mineralogy, Kyoto University. Isotope values are expressed as a per-mil difference between the sample and the PDB standard in delta notation. External precision for the standard material was better than 0.1‰.

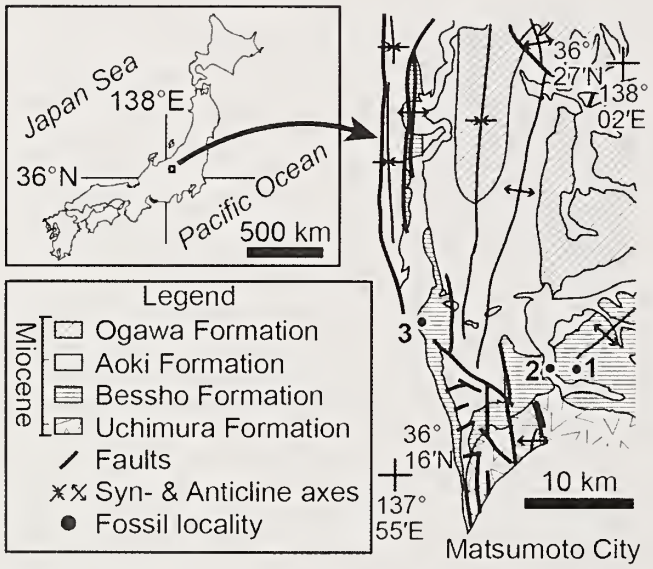
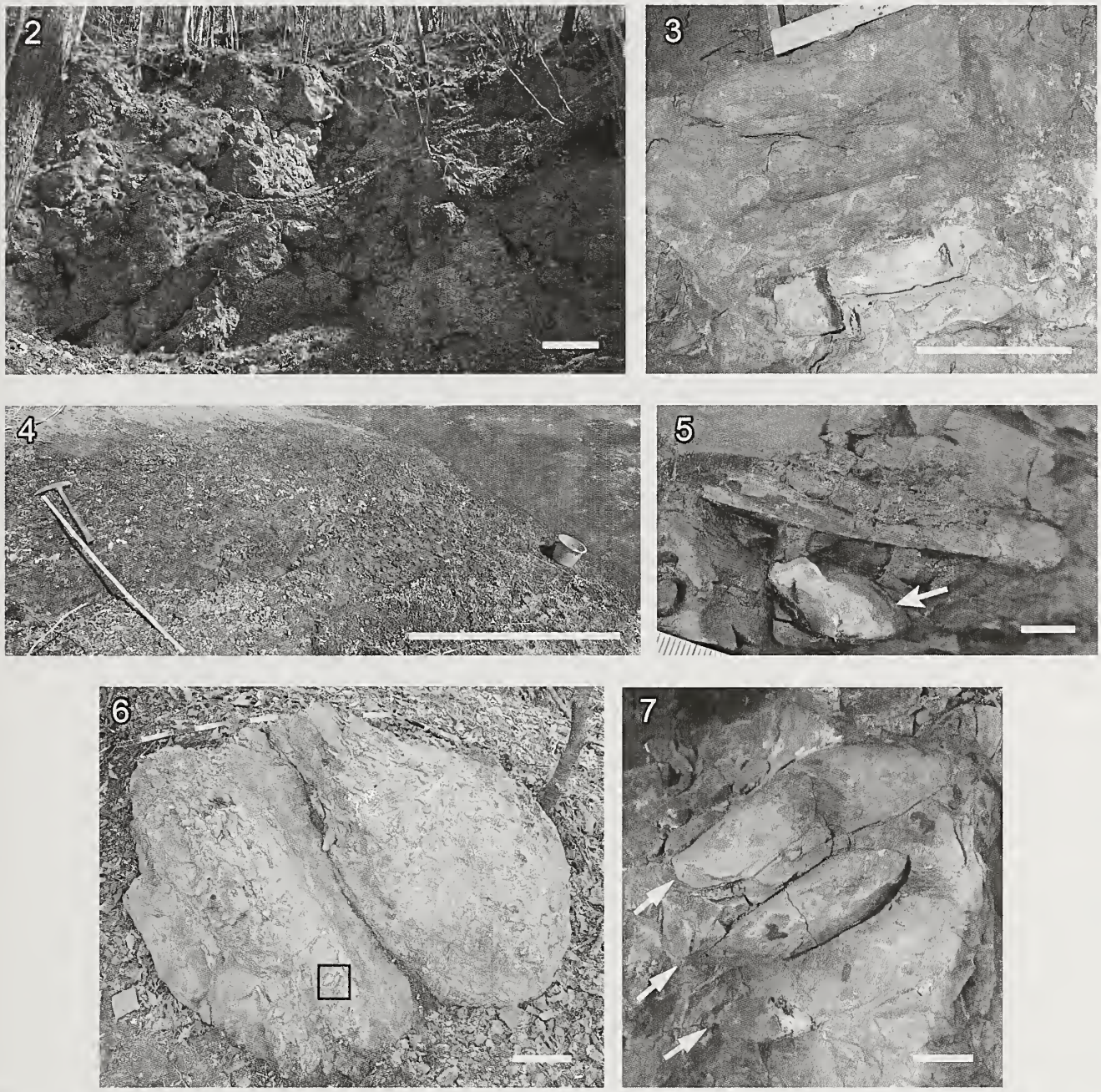


Figure 1. The geological map of the northern area of Matsumoto City, Nagano Prefecture (modified from Seki, 1983; Yamada et al., 1989; Nakano et al., 1998; Harayama et al., 2009) showing the localities of the vesicomyid fossils described herein. 1: Anazawa and Akanuda limestones. 2: Sorimachi. 3: Tonohara.

LITHOLOGY AND MODE OF FOSSIL OCCURRENCE

Seep carbonate size, lithology, and mode of fossil occurrence differ among the studied localities. At Akanuda and Anazawa (Loc. 1), large-sized seep-carbonate mounds, up to 20 m in diameter, are intercalated within the dark-gray massive siltstone (Figure 2). The carbonate mounds consist of muddy micrite with sparitic veins and veinlets, both showing low $\delta^{13}C$ values (−40 to −36‰ vs. PDB; Sato et al., 1993) originating from the anaerobic oxidation of methane (Peckmann and Thiel, 2004). These seep carbonates yield abundant molluscan fossils dominated by a large and elongate vesicomyid, *Adulomya uchimuraensis*, with patchy clusters of a bathymodiolin mussel, "*Bathymodiolus*" *akanudaensis* (Tanaka, 1959) (Tanaka, 1959; Kanno et al., 1998; Nobuhara et al., 2008; Nobuhara, 2010). In addition, the fossil fauna of the seep carbonates at this locality is characterized by a high species diversity, including bivalves *Conchocele bisecta* (Conrad, 1849), *Lucinoma* sp., and *Megathracia* sp., and gastropods *Provanna* sp., *Margarites* sp., *Comitas* sp., and *Trophonopsis* sp. The vesicomyid *A. uchimuraensis* and "*B.*" *akanudaensis* often form shell clusters composed of conjoined valves, indicating *in-situ* burial of the colonies (Figure 3). Tanaka (1959) described *Calyptogena akanudaensis* from Akanuda, but we failed to collect new specimens of this species from this locality, suggesting that it is a rare species. Tanaka (1959) also reported the bivalves *Paphia* sp. and *Liocyma* cf. *terrera* from Akanuda, both of which are here redescribed as a new vesicomyid species, *Pliocardia*? *tanakai* new species. We found seven additional specimens of this species, three of which were collected from the marginal part of the carbonate mound at Anazawa.

At Sorimachi (Loc. 2), located about 1.3 to 1.5 km west of Loc. 1, dark-gray siltstone containing small carbonate concretions, several centimeters in diameter, is exposed on a riverside cliff of the Hofukuji River (Figure 4). The carbonate concretions show $\delta^{13}C$ values as low as −35‰,



Figures 2–7. Study outcrops. **2.** Large seep carbonate body at Anazawa, Loc. 1. Scale bar = 1 m. **3.** Cluster of articulated valves of *Adulomya uchimuraensis* Kuroda in the carbonate body at Loc. 1. Scale Bar = 0.1 m. **4.** Siltstone containing abundant small carbonate concretions at Sorimachi, Loc. 2. Scale bar = 1 m. **5.** Single articulated valves of *Adulomya* sp. 1 contained in the siltstone at Loc. 2. White arrow points a carbonate concretion. Scale bar = 10 mm. **6.** Carbonate block at Tonohara, Loc. 3. Square indicates three fossils of *A. akanudaensis* enlarged in **7**. Scale bar = 0.2 m. **7.** Cluster of three articulated valves of *A. akanudaensis* (Tanaka) contained in the carbonate block at Loc. 3. White arrows indicate each fossil and its anterior direction. Note that all valves are arranged in parallel with their anterior sides in similar directions. Scale bar = 10 mm.

suggesting methane seepage at this site (details will be reported elsewhere). Mostly conjoined shells of small and elongated vesicomyid fossils are scattered throughout the siltstone, with their commissure planes parallel to the bedding plane (Figure 5). The species composition at Loc. 2 is monotonous and consists mainly of this vesicomyid, with rare lucinid and solemyid bivalves. Although the vesicomyid fossils from this locality were once identified as *Adulomya uchimuraensis* by Tanaka (1960) and Seki (1983), we show that they are distinguishable from *A. uchimuraensis* and report them in open nomenclature, as *Adulomya* sp. 1.

At Tonohara (Loc. 3), a carbonate body of ~1.1 m diameter is exposed on a slope (Figure 6). This carbonate body is entirely micritic, lacks sparitic cement, and has $\delta^{13}C$ values ranging from −29.8 to +10.5‰. Those parts of the carbonate body having positive $\delta^{13}C$ values could have originated from the ^{13}C-enriched CO_2 pool in the methanogenesis zone (Irwin et al., 1977), whereas those parts showing negative and low $\delta^{13}C$ values could have formed via the anaerobic oxidation of methane, suggesting that this locality was affected by methane seepage. This carbonate body contains *Adulomya uchimuraensis*, "*Calyptogena*" *akanudaensis*, *Conchocele* sp., and gastropod fossils. The species composition is similar to that of the large carbonate mounds at Akanuda and Anazawa (Loc. 1), but it differs from the latter in 1) "*C.*" *akanudaensis* and *A. uchimuraensis* being about equally abundant, and 2) having a lower species diversity lacking *Bathymodiolus*, *Pliocardia*, and *Provanna*. Most bivalve fossils are conjoined and often found in *in-situ* burial mode, in which all valves are arranged in parallel with their anterior sides in similar directions (Figure 7).

SYSTEMATIC PALEONTOLOGY

Family Vesicomyidae Dall and Simpson, 1901
Subfamily Pliocardiinae Woodring, 1925

Genus *Pliocardia* Woodring, 1925

Type Species: *Anomalocardia bowdeniana* Dall, 1903 from the upper Pliocene Bowden Formation in Jamaica (original designation).

Remarks: Krylova and Janssen (2006) redefined the genus *Pliocardia* as small- to medium-sized elliptical vesicomyid characterized by a shallow radial depression from umbo to postero-ventral margin, a deep lunular incision, a shallow pallial sinus, and a stout ventral tooth (1) overlying the subumbonal cardinals (3a, 3b) in the right valve. *Pliocardia* is similar to *Vesicomya* in its small shell size, clearly incised lunule, and dentition (Woodring, 1925), but differs from the latter by having thicker shells and a much thicker posterior cardinal tooth (Amano and Kiel, 2007). *Pliocardia* is also similar to *Archivesica* Dall, 1908 in dentition, but distinguished from the latter by having a much smaller shell and an escutcheon, and lacking a subumbonal pit (Amano and Kiel, 2007, 2010; Krylova et al., 2014).

Recently, Martin and Goffredi (2012) acknowledged a need for a taxonomic revision of *Pliocardia*. They newly described "*Pliocardia*" *krylovata* from the Costa Rica Margin based on molecular evidence. "*Pliocardia*" *krylovata* has a thick shell, a shallow postero-ventral depression, a shallow lunular incision, a shallow but complex pallial sinus, and a remarkably deep escutcheon. The latter two characters have not yet been recognized in *Pliocardia* (sensu stricto).

Pliocardia? *tanakai* new species
(Figures 8–23)

Liocyma cf. *terrera* (Yokoyama).—Tanaka, 1959: 121–122, pl. 3, figs. 21–22.
Paphia sp. Tanaka, 1959: 122, pl. 3, fig. 23.

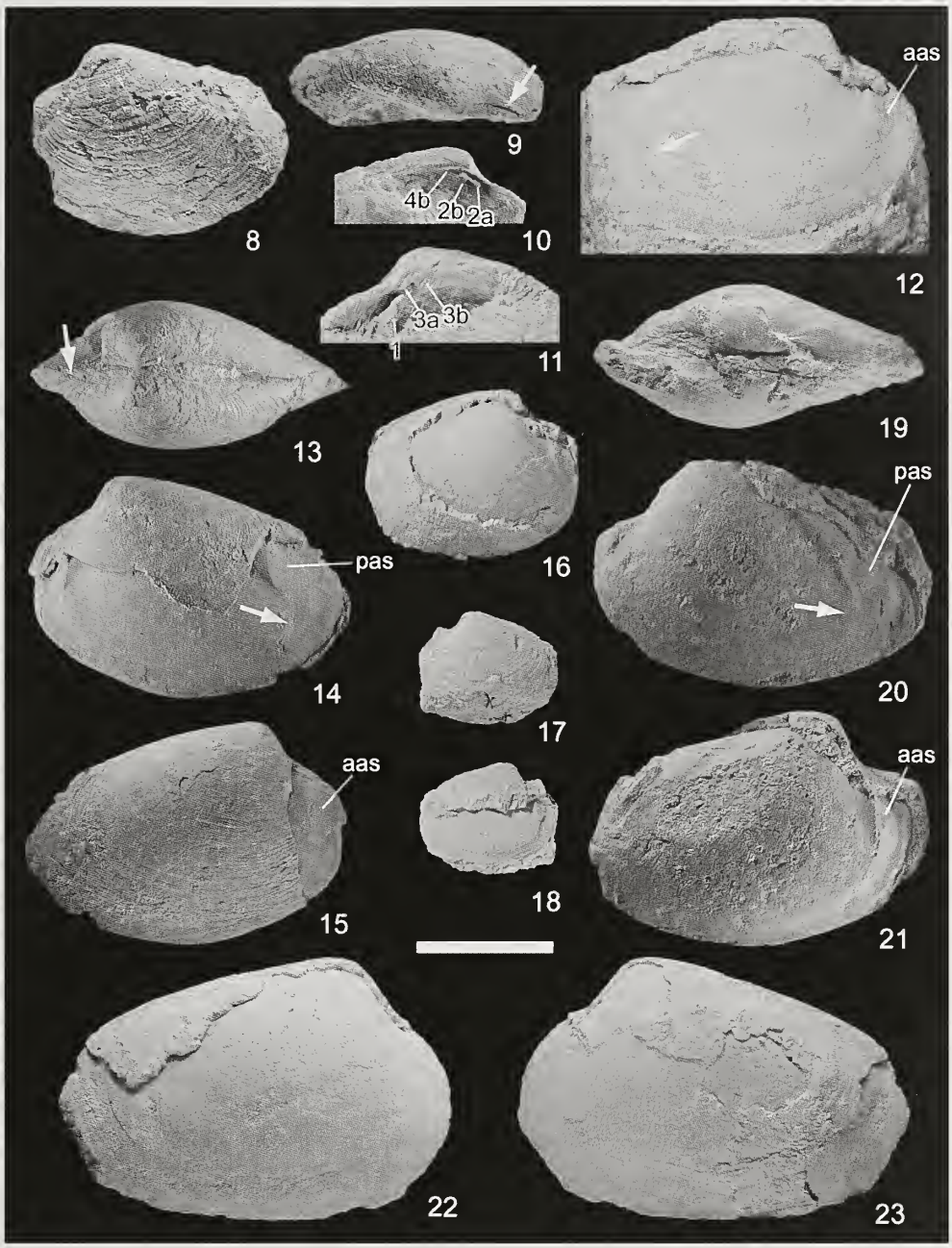
Diagnosis: Small-sized ovate vesicomyid with pointed posterior end in adult, well-defined lunular incision, ventral cardinal tooth (1) thick and anterior cardinal tooth (3a) very short in right valve hinge, anterior cardinal tooth (2a) thin and middle cardinal tooth (2b) knob-shaped, both connected at nearly right angle in their proximal parts just below umbo in left valve hinge, a blunt ridge from umbo to postero-ventral corner on internal surface but no radial depression on external surface which corresponds to the internal blunt ridge, pallial sinus lacking.

Description: Shell thin, small in size (up to 28.4 mm in length), ovate in outline (height/length = 0.57–0.78), more rounded in juvenile (length < 16 mm), equivalve and inequilateral, moderately inflated (width/length = 0.28–0.55), ornamented with fine commarginal growth lines. Antero-dorsal margin slightly concave, continuing to rounded and slightly convex anterior margin; postero-dorsal margin nearly straight, obtusely angulate at transition to posterior margin; posterior margin rounded in juvenile but more pointed with growth; ventral margin broadly arcuate. Beak prominent, prosogyrate and located at 26–38% of shell length from anterior end. Lunule well defined by distinct lunular incision. Escutcheon narrow and shallowly depressed. Right valve hinge: ventral cardinal tooth (1) moderately thick, subparallel to antero-dorsal shell margin, overlain by anterior cardinal tooth (3a) in its posterior end; anterior cardinal (3a) very short, parallel to shell margin; entire shape of posterior cardinal (3b) unclear due to recrystallization of the shell. Left valve hinge: anterior cardinal (2a) thin, parallel to antero-dorsal shell margin; middle cardinal (2b) short and knob-shaped, situated just below umbo, connected with anterior cardinal (2a) at nearly right angle in their proximal parts; posterior cardinal (4b) slightly thinner but as long as anterior cardinal (2a), subparallel to postero-dorsal shell margin, detached from other cardinals (2a and 2b). Anterior adductor muscle scar ovate with rather straight and deeply impressed posterior margin. Posterior adductor muscle scar ovate with deeply impressed anterior margin forming a blunt inner ridge running from beak. Pallial line entire, starting at postero-ventral corner of anterior adductor scar and connecting to antero-ventral corner of posterior adductor scar without pallial sinus.

Measurements: See Table 1.

Holotype: Right valve preserving its dentition and adductor muscle scars with pallial line on internal mold, SFMCM-0182 (Figures 11 and 12).

Paratypes: One left valve with its dentition preserved, SFMCM-0178 (Figures 8–10); four closed valves partly



Figures 8–23. *Pliocardia*? *tanakai* new species. All specimens are from Loc. 1. **8–10.** Lateral (**8**) and dorsal (**9**) views, and hinge (**10**) of left valve; Paratype, SFMCM-0178. White arrow shows lunular incision. **11–12.** Right valve hinge (**11**) and inner mold of right valve (**12**); **aas**, anterior adductor muscle scar; Holotype, SFMCM-0182. White arrow shows lack of pallial sinus. **13–15.** Dorsal (**13**), left lateral (**14**) and right lateral (**15**) views; **aas**, anterior adductor muscle scar; **pas**, posterior adductor muscle scar; Paratype, SFMCM-0180. White arrows show lunular incision (**13**) and lack of pallial sinus (**14**). **16.** Right lateral view with inner mold in part; Paratype, SFMCM-0181. **17–18.** Left lateral view (**17**) and right lateral view with inner mold in part (**18**); Paratype, SFMCM-0183. **19–21.** Dorsal view (**19**), left lateral (**20**) and right lateral (**21**) views of inner mold; **aas**, anterior adductor muscle scar; **pas**, posterior adductor muscle scar; Paratype, SFMCM-0179. White arrow shows lack of pallial sinus. **22–23.** Right lateral (**22**) and left lateral (**23**) views of inner mold; SFMKT-00399. Scale bar = 10 mm (for all figures).

exhibiting internal molds with adductor scars and pallial lines, SFMCM-0180 (Figures 13–15), 0181 (Figure 16), 0183 (Figures 17 and 18), 0179 (Figures 19–21).

Other Examined Material: One inner mold of both valves, SFMCM-0184; three conjoined valves from Loc. 1, which were once described by Tanaka (1959) as *Liocyma* cf. *terrera* (No. 520 in Tanaka, 1959, pl. III, figs. 21 and 22), registered now as SFMKT-00398, and *Paphia* sp. (No. 521 in Tanaka, 1959, pl. III, fig. 23), registered now as SFMKT-00399.

Table 1. Measurements of *Pliocardia*? *tanakai* new species from Loc. 1.

Specimen number	Type	Length (mm)	Height (mm)	Width (mm)	H/L	W/L	Valve
SFMCM-0178	Paratype	18.0+	13.2	-	-	-	left
SFMCM-0179	Paratype	24.6	16.3	9.9	0.66	0.40	both
SFMCM-0180	Paratype	23.5	15.8	10.0	0.67	0.43	both
SFMCM-0181	Paratype	15.9	12.3	7.3	0.77	0.46	both
SFMCM-0182	Holotype	24.2+	16.2	-	-	-	right
SFMCM-0183	Paratype	10.2	8	5.6	0.78	0.55	both
SFMCM-0184		17.4	12.7	7.8	0.73	0.45	both
SFMKT-00398-1		18.9+	13.0	7.4	-	-	both
SFMKT-00398-2		20.8	12.0	5.8	0.57	0.28	both
SFMKT-00399		28.4	18.6	12.8	0.66	0.45	both

Type Locality: Akanuda and Anazawa, Matsumoto City, Nagano Prefecture, central Japan (Loc. 1 in Figure 1).

Distribution: Only from the type locality, middle Miocene Bessho Formation in Nagano Prefecture, central Japan.

Etymology: Named after the Emeritus Professor Kunio Tanaka, who made great contributions to the geology and paleontology of Nagano Prefecture.

Remarks: The present species is tentatively assigned to the genus *Pliocardia* because of its ovate shell outline, a right valve hinge having stout ventral cardinal (1) and arched subumbonal cardinals (very short 3a and 3b), and a distinct lunular incision, which are the diagnostic characters of the genus *Pliocardia* as redefined by Krylova and Janssen (2006). However, this species lacks the following two diagnostic characters: 1) a shallow pallial sinus and 2) a radial depression on the external shell surface running from the umbo to the postero-ventral margin. Considering that the genus *Pliocardia* is taxonomically uncertain at present as mentioned by Martin and Goffredi (2012), we avoid at this point erection of a new genus for this species.

This species is also similar to the species of *Waisiuconcha* Beets, 1942, in its ovate or subcircular shell outline, strong ventral cardinal (1) and arched subumbonal cardinals (3a and 3b) in the right valve hinge, well-defined lunular incision, and lacking of a pallial sinus (Cosel and Salas, 2001). *Waisiuconcha* has, however, a pallial line distant from the ventral margin, while the present species has a pallial line close to the ventral margin. Moreover, *Waisiuconcha* also lacks a radial depression or an inner ridge on the shell surface.

Pliocardia? *tanakai* new species resembles the type species of the genus *Austrogena* Krylova, Sellanes, Valdés, and D'Elía, 2014, which was recently described from the Chilean margin, in the presence of a lunule and an escutcheon, its hinge dentitions of both valves, and the absence of a pallial sinus. The genus *Austrogena*, however, has an oval to more rectangular shell and a less impressed lunular incision than *P.*? *tanakai*. Moreover, the hinge plate of adult *Austrogena* is characterized by the presence of a subumbonal pit, which is absent in *P.*? *tanakai*. *Austrogena* is known only from the southeastern Pacific at present (Krylova et al., 2014).

The genus *Notocalyptogena* Amano, Saether, Little, and Campbell, 2014 also has a radial internal ridge similarly to *Pliocardia*? *tanakai*. However, *Notocalyptogena* can be clearly distinguished from the present species by its larger, elongate shell, a longer anterior cardinal tooth (3a) in the right valve, and lacking a lunule.

Pliocardia? *tanakai* is the second Japanese fossil species assignable to this genus. *Pliocardia kawadai* (Aoki, 1954) has been known as the only Japanese fossil species of this genus, and it has been reported from the lower to middle Miocene seep and whale-fall sites in the central to northern Japan (Amano and Kiel, 2012).

Comparisons: *Pliocardia*? *tanakai* new species can be clearly distinguished from the other two Japanese *Pliocardia* species, i.e., *P. kawadai* from the lower to middle Miocene and the living species *P. crenulomarginata* (Okutani, Kojima and Iwasaki, 2002), by having a smaller and lower shell (Figure 24) and by lacking a pallial sinus and a distinct radial depression from the beak to the postero-ventral corner on the external shell surface.

Pliocardia? *tanakai* resembles *Pliocardia*? sp. from the upper Oligocene part of the Lincoln Creek Formation in western Washington State, USA (Amano and Kiel, 2007, 2012) in shell size and outline, but differs from it in lacking a depressed area running from the beak to the posterior corner on the external shell surface and in having a weaker anterior cardinal tooth (3a) in the right valve.

Amano and Kiel (2012) suggested that some of the Paleogene vesicomyid species from the North Pacific realm which were previously assigned to *Archivesica*, including the oldest known vesicomyid "*Archivesica*" cf. *tschudi* (Olsson, 1931) from the upper middle Eocene Humptulips Formation in western Washington, USA, may belong to *Pliocardia*. *Pliocardia*? *tanakai* resembles "*A*". cf. *tschudi* illustrated in Amano and Kiel (2007) in having an ovate shell outline, an inner ridge just before the posterior adductor muscle scar, and no pallial sinus, but is distinct from the latter by a more posteriorly situated beak, a non-undulated anterior cardinal tooth (2a), and lacking of a subumbonal pit. *P.*? *tanakai* is also similar to *Vesicomya* aff. *tschudi* Olsson, 1931 reported

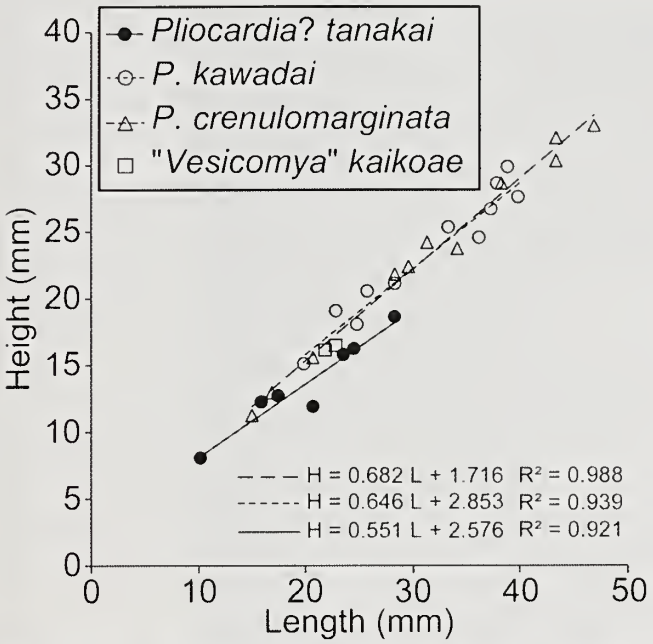

Pliocardia? tanakai
P. kawadai
P. crenulomarginata
"Vesicomya" kaikoae
Height (mm)
Length (mm)
H = 0.682 L + 1.716 R² = 0.988
H = 0.646 L + 2.853 R² = 0.939
H = 0.551 L + 2.576 R² = 0.921

Figure 24. Relationships between shell length and height with growth of *Pliocardia*? *tanakai* new species, *P. kawadai* (Aoki), *P. crenulomarginata* (Okutani, Kojima and Iwasaki), and "*Vesicomya*" *kaikoae* Okutani, Fujikura and Kojima. Measurements of *P. kawadai* are from Kamada (1962) and Amano et al. (2001), those of *P. crenulomarginata* are from Krylova and Janssen (2006), and those of "*V*". *kaikoae* are from Okutani et al. (2000).

by Squires and Gring (1996) from the upper Eocene Wagonwheel Formation in California, USA, in its shell size and shape. Although the specimens of Squires and Gring (1996) did not show the hinge characters and seems to be somewhat deformed, they are clearly distinguishable from *P.*? *tanakai* by a truncated posterior end.

Pliocardia? *tanakai* also resembles *Pliocardia*? sp. from the lower to middle Miocene Bexhaven Limestone, New Zealand (Amano et al., 2014) in its shell outline with a subtruncated posterior margin, a lunular incision, and a blunt ridge running from the beak to the postero-ventral corner, but differs from the latter species in lacking a pallial sinus. Moreover, the posterior cardinal tooth (3b) of *P.*? *tanakai* is not as strong as that of *Pliocardia*? sp. from the Bexhaven Limestone.

Some specimens of *Calyptogena pacifica* Dall, 1891 from the upper Miocene in Japan (Amano and Jenkins, 2011) have an ovate shell outline like *Pliocardia*? *tanakai*. *Calyptogena pacifica* also has an escutcheon and lacks a pallial sinus, but can be distinguished from *P.*? *tanakai* by having a less inflated shell and lacking a lunule.

Pliocardia? *tanakai* resembles the Recent "*Vesicomya*" *kaikoae* Okutani, Fujikura and Kojima, 2000 in shell size and outline (Figure 24), the presence of a lunular incision, and the right valve dentition having a ventral tooth (1) overlaid by arched cardinals (3a and 3b). But "*Vesicomya*" *kaikoae* has a pallial line with a shallow embayment which is absent in *P.*? *tanakai*. Recently, molecular phylogenetic analyses revealed that "*V*". *kaikoae* is well separated from the other vesicomyid species including *Pliocardia* species (Kojima et al., 2004; Krylova and Sahling, 2010; Decker et al., 2012).

Genus *Adulomya* Kuroda, 1931

Type Species: *Adulomya uchimuraensis* Kuroda, 1931 from the middle Miocene Bessho Formation in central Honshu, Japan (monotypy).

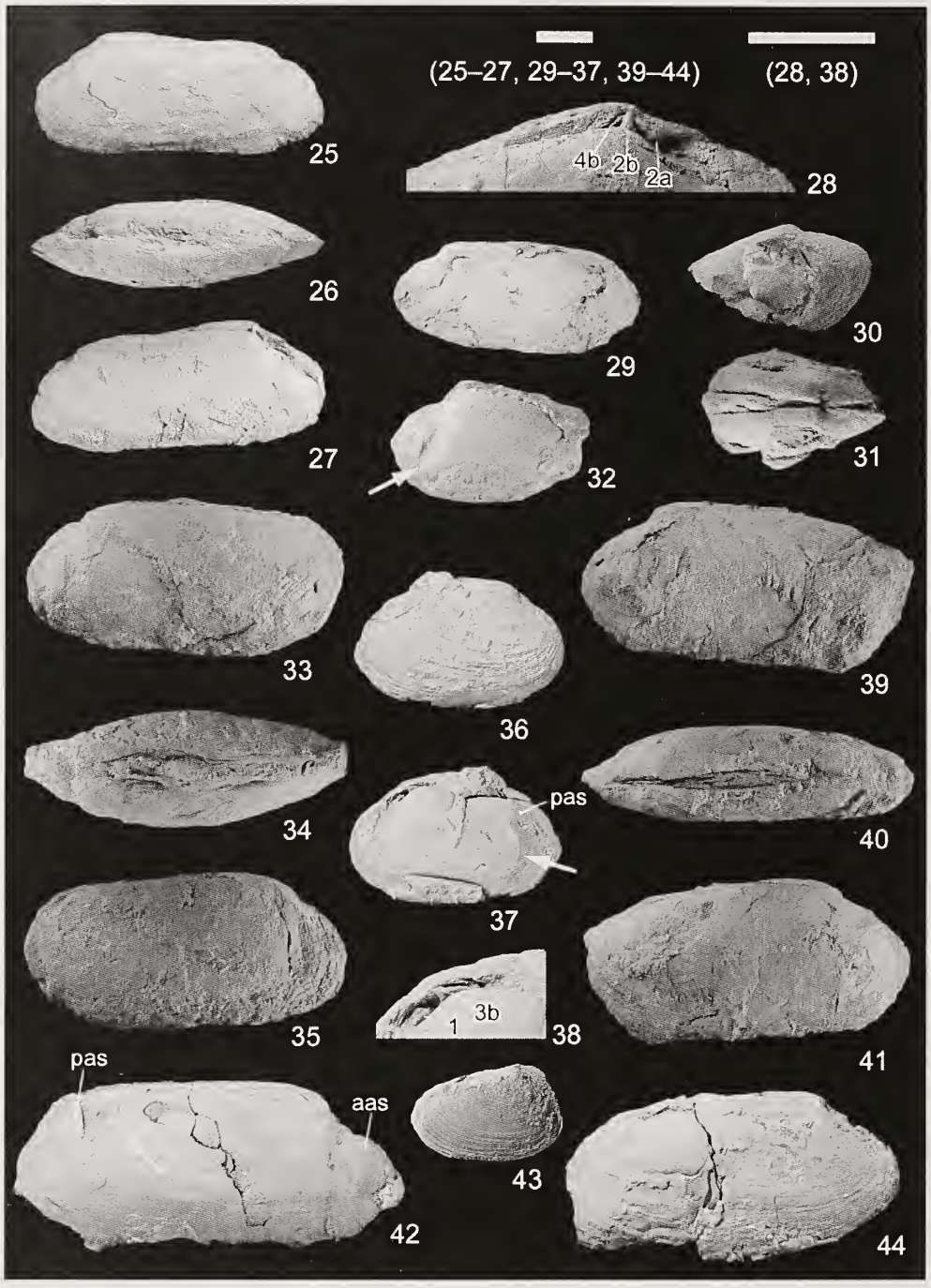
Remarks: The genus *Adulomya* was redefined by Amano and Kiel (2007) and characterized by its elongate shell, two radiating cardinal teeth in the right valve hinge, and lacking of a pallial sinus except for *A. chitanii* Kanehara, 1937 (Amano and Kiel, 2011). *Adulomya* first appeared in the eastern Pacific in late Eocene age (Amano and Kiel, 2007) and invaded into Japan in the early Miocene (Amano and Kiel, 2011). Japanese *Adulomya* showed its high species diversity during early to middle Miocene in lower sublittoral to middle bathyal depths, but declined with replacement by other vesicomyid genera such as *Archivesica* and *Calyptogena* since the late Miocene (Amano and Kiel, 2011).

Adulomya akanudaensis (Tanaka, 1959) new combination

(Figures 25–44)

Calyptogena akanudaensis Tanaka, 1959: 119–120, pl. 2, figs. 1–9; Amano and Kiel, 2011: 84, figs. 27–29.

Redescription: Shell thin, moderate in size (up to 71.1 mm long), elongated elliptical in shape (height/length = 0.39–0.68), equivalve and inequilateral, slightly to moderately inflated (width/length = 0.24–0.40), sculptured by fine commarginal growth lines with wider interspaces in posterior part. Antero-dorsal margin nearly straight to slightly concave, graduating to rounded or slightly protruded anterior margin; postero-dorsal margin nearly straight and parallel to ventral margin or slightly convex, continuing to rounded posterior margin; ventral margin straight, broadly arcuate in juvenile (length < 27 mm), or slightly concave at its central part in some specimens. Beak low, prosogyrate, and situated at 16–40% of shell length from anterior margin. Lunule and escutcheon absent. Right valve hinge: anterior cardinal tooth (3a) reduced; central cardinal tooth (1) small, triangular, situated below umbo, with hollow space between its dorsal end and umbo; posterior cardinal tooth (3b) moderately thick, bifid, subparallel to postero-dorsal shell margin, detached from central cardinal tooth (1). Left valve hinge: anterior cardinal tooth (2a) thick, oblique anteriorly, connecting with central cardinal tooth (2b) in their proximal parts at acute angle; central cardinal tooth (2b) stout, situated just below umbo, tapered to proximal part, nearly perpendicular to hinge base; posterior cardinal tooth (4b) thin, weak, oblique posteriorly, connecting with central cardinal tooth (2b) as with



Figures 25–44. *Adulomya akanudaensis* (Tanaka). Specimens of Figures 25–35 and 39–41 are from Loc. 1 (type locality) and those of Figures 36–38 and 42–44 are from Loc. 3. **25–28.** Left lateral view (**25**), dorsal view (**26**), and right lateral view of inner mold (**27**), and left valve hinge (**28**); Neotype, SFMKT-00404. **29.** Left lateral view with inner mold; Paratype, SFMKT-00401. **30–31.** Right lateral view of a small specimen, SFMKT-00405-1 (paratype), attached on a large specimen, SFMKT-00405-2 (**30**), and dorsal view of a large specimen, SFMKT-00405-2 (**31**). **32.** Left lateral view with inner mold; Paratype, SFMKT-00406. White arrow shows inner rib. **33–35.** Left lateral (**33**), dorsal (**34**), and right lateral (**35**) views; Paratype, SFMKT-00403. **36–38.** Right lateral view (**36**), left lateral view of inner mold (**37**), and right valve hinge (**38**); pas, posterior adductor muscle scar; SFMCM-0191. White arrow shows lack of pallial sinus. **39–41.** Left lateral view of inner mold (**39**), dorsal view (**40**), and right lateral view of inner mold (**41**); Paratype, SFMKT-00402. **42.** Right lateral view of inner mold; aas, anterior adductor muscle scar; pas, posterior adductor muscle scar; SFMCM-0185. White arrow shows inner ridge. **43.** Right lateral view; SFMCM-0189. **44.** Right lateral view; SFMCM-0188. Scale bars = 10 mm (for all figures).

anterior cardinal tooth (2a). Anterior adductor muscle scar well impressed and ovate, with a distinct inner rib running from beak to base of posterior margin of anterior adductor scar. Posterior adductor muscle scar ovate and indistinct except for its anterior margin, with a blunt inner ridge running from postero-dorsal shell margin to antero-ventral corner of posterior adductor scar. Pallial line indistinct in ventral part, starting at postero-ventral corner of anterior adductor scar and connecting with antero-ventral corner of posterior adductor scar without pallial sinus.

Measurements: See Table 2.

Type Material: The holotype was originally designated and illustrated by Tanaka (1959, pl. II, figs. 5 and 6, a specimen "No. 510"). Specimens SFMKT-00389 in the Kunio Tanaka's collection at the Shinshushinmachi Fossil Museum are with an original label "No. 510", but all of the specimens are clearly different from the illustrated holotype. Moreover, we could not find any specimens corresponding to the holotype illustration in the collection. We therefore judge that the holotype is lost and designate a neotype as a conjoined valve preserving the left hinge dentition (Figures 25–28), SFMKT-00404 (No. 527 in Tanaka, 1959, one of his paratypes); six paratypes excluding SFMKT-00404 designated in Tanaka (1959), i.e., SFMKT-00144 (No. 255 in Tanaka, 1959, pl. II, figs. 1–4), SFMKT-00401 (No. 524, pl. II, fig. 8), SFMKT-00402 (No. 525, pl. II, fig. 9), SFMKT-00403 (No. 526, pl. II, fig. 7), SFMKT-00405 (No. 528), SFMKT-00406 (No. 529), and SFMKT-00407 (No. 530). Tanaka (1959) also designated No. 531 (SFMKT-00408) as a paratype, but it was identified as another species, *Adulomya uchimuraensis*.

Type Locality: Akanuda, Matsumoto City, Nagano Prefecture, central Japan (Loc. 1 in Figure 1).

Table 2. Measurements of *Adulomya akanudaensis* (Tanaka) from Loc. 1 and 3.

Specimen number	Type	Length (mm)	Height (mm)	Width (mm)	H/L	W/L	Valve	Loc.
SFMKT-00144	Paratype	54.4+	26.8	-	-	-	right	1
SFMKT-00401	Paratype	42.3	18.8	-	0.44	-	both	1
SFMKT-00402	Paratype	57.4+	27.7	16.1+	-	-	both	1
SFMKT-00403	Paratype	55.6	27.7	19.9+	0.50	-	both	1
SFMKT-00404	Neotype	51.1	21.6	14.9	0.42	0.29	both	1
SFMKT-00405-1	Paratype	9.6+	5.5	-	-	-	both	1
SFMKT-00405-2		32.1+	21.1+	-	-	-	both	1
SFMKT-00406	Paratype	34.6+	22.1	15.3	-	-	both	1
SFMCM-0185		67.9	29.8	22.1	0.44	0.33	both	3
SFMCM-0186		45.7	19.8	11.0	0.43	0.24	both	3
SFMCM-0187		51.4	21.9	-	0.43	-	right	3
SFMCM-0188		59.8	29.3	17.5	0.49	0.29	both	3
SFMCM-0189		27.4	17.0	9.2	0.62	0.34	both	3
SFMCM-0190		65.5	34.3	-	0.52	-	both	3
SFMCM-0191		38.1	23.4	15.1	0.61	0.40	both	3
SFMKT-07227		38.8+	20.4	11.9	-	-	both	3
SFMKT-07228-1		22.1	12.9	7.9	0.58	0.36	both	3
SFMKT-07228-2		24.6	14.8	7.1	0.60	0.29	both	3
SFMKT-07228-3		10.0	6.8	-	0.68	-	right	3
SFMKT-07229-1		23.7	14.3	7.9	0.60	0.33	both	3
SFMKT-07229-2		20.6+	12.4	8.1	-	-	both	3
SFMKT-07229-3		20.7+	12.2	6.7	-	-	both	3
SFMKT-07230-1		56.0	21.7	15.3	0.39	0.27	both	3
SFMKT-07230-2		31.2+	17.9	-	-	-	right	3
SFMKT-07230-3		41.4+	21.0	-	-	-	left	3
SFMCM-0156		63.2	29.0	-	0.46	-	both	3
SFMCM-0157		38.9	16.3	10.5	0.42	0.27	both	3
SFMCM-0158		37.1	17.1	10.4	0.46	0.28	both	3
SFMCM-0162		29.3	13.4	7.5	0.46	0.26	both	3
SFMCM-0164		53.1	25.0	20.3	0.47	0.38	both	3
SFMCM-0165		65.7	29.7	22.6	0.45	0.34	both	3
SFMCM-0166		53.2	23.0	16.5	0.43	0.31	both	3
SFMCM-0167		66.1	29.6	-	0.45	-	both	3
SFMCM-0168		63.6	29.0	-	0.46	-	left	3
SFMCM-0169		71.1	32.9	25.1	0.46	0.35	both	3
SFMCM-0170		46.9	22.5	15.0	0.48	0.32	both	3
SFMCM-0171		28.5	15.0	9.4	0.53	0.33	both	3

Other Examined Material: In addition to type materials from Loc. 1 (SFMKT-00401 to 00407), more than fifty specimens were collected from Loc. 3 and twenty-nine well-preserved specimens of them were measured and examined, SFMCM-0185 to 0191, SFMKT-07227 to 07230, SFMCM-0156 to 0158, 0162, and 0164 to 0171.

Remarks: This species was originally described by Tanaka (1959) as *Calyptogena akanudaensis*, which is distinct from the sympatric vesicomyid *Adulomya uchimuraensis* by its less elongated shell outline. The generic assignment of this species has been pointed out to be problematic because its internal shell characters were unknown (Amano and Kiel, 2011). We reexamined the paratypes and succeeded in exposing the left valve hinge consisting of three cardinals, 2a, 2b, and 4b (Figure 2B). Moreover, we obtained many additional specimens from Loc. 3 and revealed that the right valve hinge is composed of two cardinals, 1 and 3b (Figure 3B). These hinge dentitions agree well with those of *Adulomya*, and are inconsistent with an assignment to *Calyptogena* Dall, 1891, which has three cardinal teeth and a posterior nymphal ridge on the right valve.

The reassignment of this species from *Calyptogena* to *Adulomya* is consistent with the temporal distribution of other vesicomyid species around the Japanese islands, which was reviewed by Amano and Kiel (2007, 2011), Amano and Jenkins (2011), and Amano (2014). According to them, *Adulomya* diversified in the middle Miocene in both the Pacific and the Japan Sea sides, whereas *Calyptogena* first appeared in the late Miocene in the Japan Sea borderland.

Comparisons: It can clearly be ruled out that *Adulomya akanudaensis* represents juvenile shells of *A. uchimuraensis*, because the former has a much higher shell than the latter (Figure 45). Moreover, juveniles of *A. akanudaensis* have ovate and more inflated shells with a less protruded anterior margin than the juveniles of *A. uchimuraensis*.

Smaller specimens of *Adulomya hamuroi* Amano and Kiel, 2011 from the uppermost lower or lowest middle Miocene in Toyama Prefecture, Japan are similar to *A. akanudaensis* in their elongated elliptical shells, but are different from *A. akanudaensis* by having a slightly higher shell with a concave ventral margin. Moreover, *A. akanudaensis* has a less stout central cardinal tooth (1) in the right valve than *A. hamuroi* and the central cardinal tooth (2b) in the left valve is not bifid as *A. hamuroi*.

Amano and Kiel (2011) pointed out that some specimens of *Adulomya akanudaensis* have similar proportions as *A. kuroiwaensis* Amano and Kiel, 2011 from the uppermost middle or lowest upper Miocene in Niigata Prefecture, Japan, but *A. kuroiwaensis* has a more anteriorly situated beak and an expanded posterior part. Based on the examined specimens of *A. akanudaensis* herein, this species has a higher shell than *A. kuroiwaensis* (Figure 45), and has a hollow space between the umbo and the central cardinal tooth (1) of the right valve that is absent in *A. kuroiwaensis*.

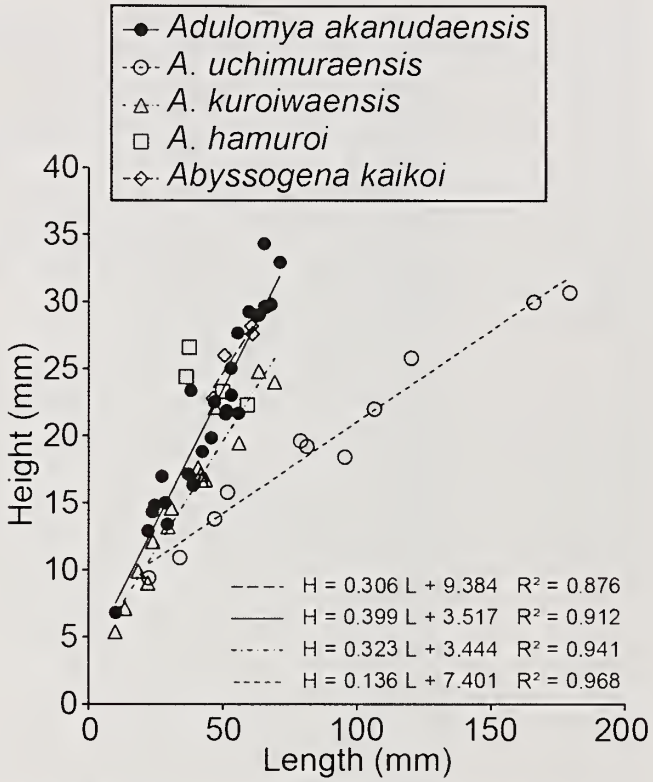


Figure 45. Relationships between shell length and height with growth of *Adulomya akanudaensis* (Tanaka) from Locs. 1 and 3, *A. uchimuraensis* Kuroda, *A. kuroiwaensis* Amano and Kiel, *A. hamuroi* Amano and Kiel, and *Abyssogena kaikoi* (Okutani and Métivier). Measurements of *A. uchimuraensis* are from Kanno et al. (1998), those of *A. kuroiwaensis* and *A. hamuroi* are from Amano and Kiel (2011), and those of *Ab. kaikoi* are from Krylova et al. (2010).

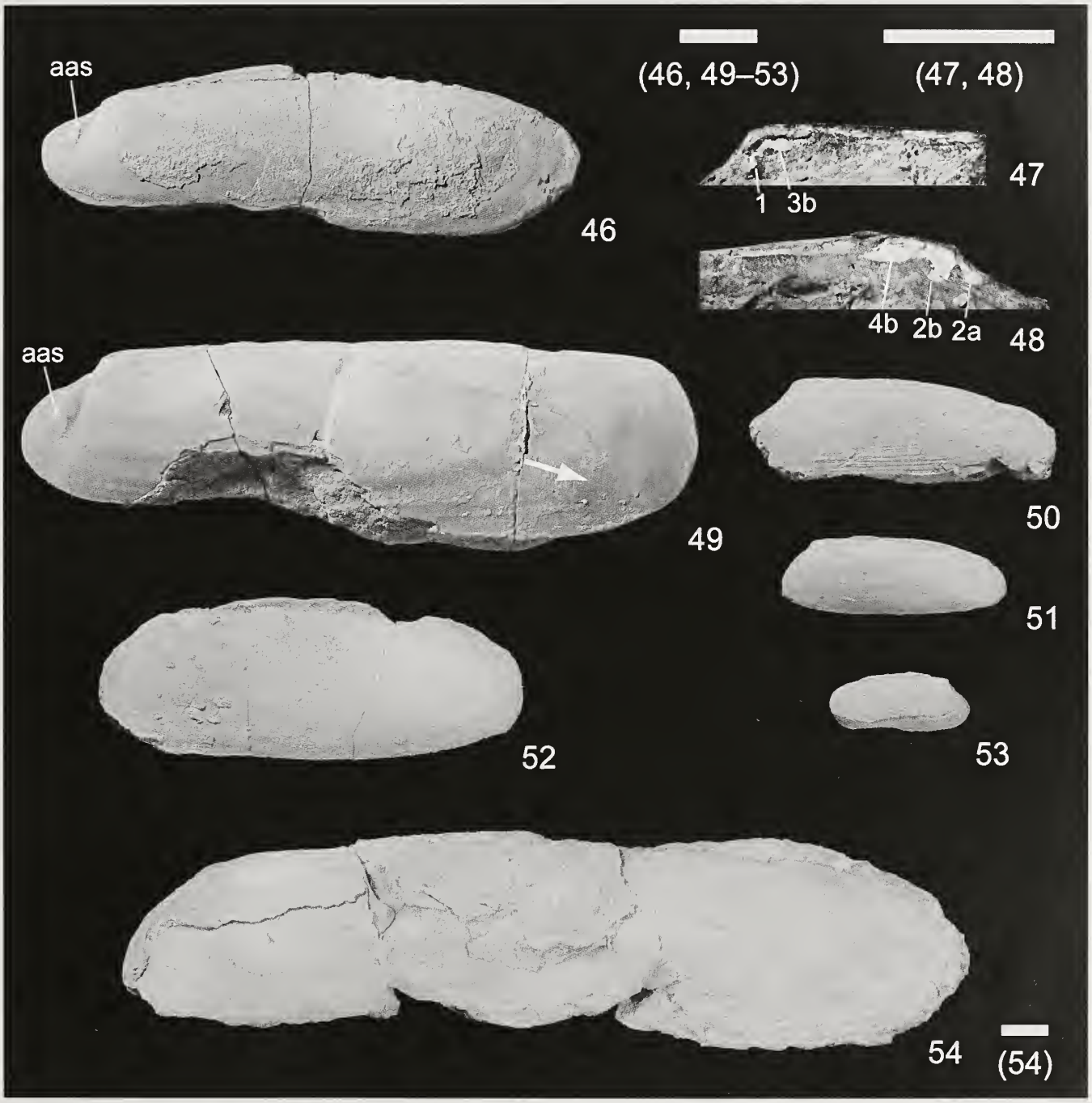
Adulomya akanudaensis resembles *A. chinookensis* (Squires and Goedert, 1991) from the upper Eocene to lower Oligocene in western Washigton, USA in general shell outline and having a blunt ridge extending posteroventrally from the umbo. *A. chinookensis* was originally described as *Calyptogena chinookensis*, but Amano and Kiel (2007) revealed its dentition and reassigned it into the genus *Adulomya*. *Adulomya akanudaensis* is different from *A. chinookensis* by having a less elongate shell and a hollow space between the central cardinal tooth (1) and the umbo in the right valve.

Adulomya akanudaensis is also similar to *Abyssogena kaikoi* (Okutani and Métivier, 1986) living in the Pacific side of Japan, in shell proportion (Figure 45) and nonfusing cardinals (1 and 3b) in the right valve. *Abyssogena kaikoi* was originally assigned to the subgenus *Ectenagena* Woodring (1938), which was later synonymized to the genus *Adulomya* by Amano and Kiel (2007). Krylova et al. (2010) established the new genus *Abyssogena* including *Abyssogena kaikoi* and stated that *Abyssogena*

differs from *Adulomya* by the absence of subumbonal pits and a pallial line originating from the ventral margin of the anterior adductor scar. *Adulomya akanudaensis* differs from *Abyssogena kaikoi* by lacking a pallial sinus and a bifid posterior cardinal tooth (3b) in the right valve.

Distribution: Middle Miocene Bessho Formation in Nagano Prefecture, Japan.

***Adulomya* sp. 1**
(Figures 46–53)



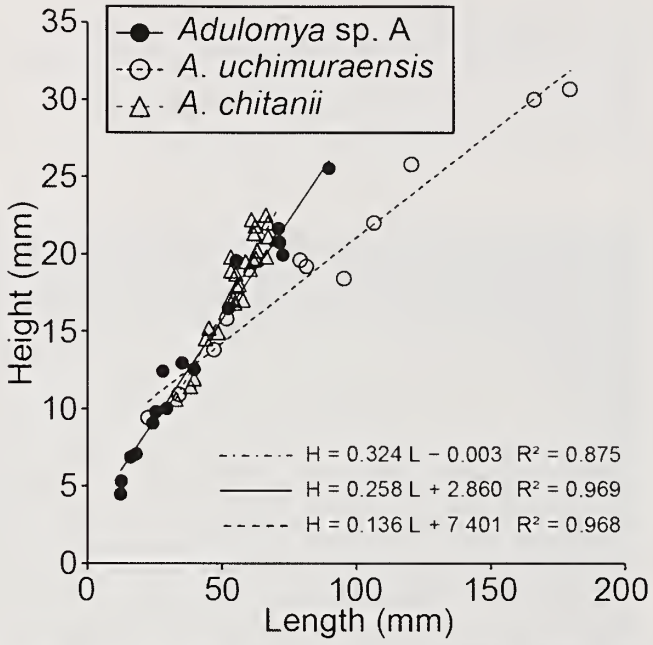
Figures 46–53. *Adulomya* species. **46–53.** *Adulomya* sp. 1. All specimens are from Loc. 2. **46.** Left lateral view of inner mold; **aas**, anterior adductor muscle scar; KUGSMM01. **47.** Right valve hinge; KUGSMM78. **48.** Left valve hinge; KUGSMM66. **49.** Left lateral view of inner mold; **aas**, anterior adductor muscle scar; KUGSMM100-6. White arrow shows lack of pallial sinus. **50.** Left lateral view; KUGSMM61. **51.** Left lateral view of inner mold; KUGSMM103. **52.** Left lateral view of inner mold; KUGSMM41. **53.** Right lateral view of inner mold; KUGSMM84. **54.** *Adulomya uchimuraensis* Kuroda from Loc. 1. Left lateral view with inner mold in part. Scale bars = 10 mm (for all figures).

Description: Shell small for genus (up to 89.9 mm long), elongate throughout ontogeny (height/length = 0.27–0.44), posteriorly expanded, equivalve and inequilateral, weakly inflated (width/length = 0.15–0.30), sculptured by fine growth lines widening in posterior part. Antero-dorsal margin nearly straight to broadly concave, gradually changing to narrowly rounded and slightly protruded anterior margin; postero-dorsal margin long and straight to broadly convex, continuing to rounded posterior margin gradually or a little abruptly at obtuse angle; ventral margin broadly arcuate or broadly concave in some specimens. Beak low, prosogyrate, situated at 7–21% of shell length from anterior margin. Lunule and escutcheon absent; ligament exterior, strong and long, occupying more than half of postero-dorsal margin. Right valve hinge: anterior cardinal tooth (3a) reduced; central cardinal tooth (1) thin, slightly oblique anteriorly from umbo; posterior cardinal tooth (3b) thick, oblique posteriorly. Left valve hinge: anterior tooth (2a) thick, subparallel to antero-dorsal shell margin, connected to central tooth (2b); central tooth (2b) as thick as anterior tooth (2a), vertical to hinge base; posterior tooth (4b) as thick as anterior (2a) and central (2b) teeth, connected to central tooth (2b), oblique posteriorly, but its distal end unknown. Anterior adductor muscle scar small and pear-shaped, with a distinct inner rib running from umbo to just below anterior adductor scar. Posterior adductor muscle scar indistinct. Pallial line only visible in posterior part, lacking pallial sinus. Indistinct radial interior striations visible in anterior part, running from umbo in slightly posterior direction.

Measurements: See Table 3.

Material Examined: Among one hundred and thirty collections from Loc. 2, sixteen entirely-preserved specimens were measured and examined, KUGSMM01, 08, 18, 41, 60, 61, 84, 92, 96, 99, 100, 101, and 103.

Distribution: Only from Sorimachi (Loc. 2), middle Miocene Bessho Formation in Nagano Prefecture, Japan.



Figures 55. Relationships between shell length and height with growth of *Adulomya* sp. 1 from Loc. 2, *A. uchimuraensis* Kuroda, and *A. chitanii* Kanehara. Measurements of *A. uchimuraensis* and *A. chitanii* are from Kanno et al. (1998) and Amano and Kiel (2011), respectively.

Remarks: The elongate shell and the hinge structures composed of two cardinals on the right and three cardinals on the left valve show that the vesicomyid fossils from Loc. 2 belong to the genus *Adulomya*. We tentatively describe them as *Adulomya* sp. 1 because of the poor preservation; most specimens are deformed and compressed inner molds or shells almost dissolved or replaced by sparry calcite, with the cardinal teeth unclear. *Adulomya* sp. 1 was previously reported as

Table 3. Measurements of *Adulomya* sp. 1 from Loc. 2.

Specimen number	Length (mm)	Height (mm)	Width (mm)	H/L	W/L	Valve
KUGSMM01	71.4	20.7	11.8	0.29	0.17	both
KUGSMM08	52.4	16.5	9.5	0.31	0.18	both
KUGSMM18	72.5	19.9	11.9	0.27	0.16	both
KUGSMM41	55.3	19.6	9.5	0.35	0.17	both
KUGSMM60	35.2	12.9	6.5	0.37	0.19	both
KUGSMM61	39.7	12.5	7.4	0.32	0.19	both
KUGSMM84	18.1	7.1	-	0.39	-	both
KUGSMM92	12.2	4.5	3.5	0.37	0.28	both
KUGSMM96	12.5	5.3	3.4	0.43	0.27	both
KUGSMM99	16.0	6.9	-	0.43	-	both
KUGSMM100-4	28.0	12.4	8.4	0.44	0.30	both
KUGSMM100-6	89.9	25.5	13.9	0.28	0.15	both
KUGSMM100-8	71.0	21.6	-	0.30	-	both
KUGSMM101-4	25.4	9.8	4.6	0.39	0.18	both
KUGSMM101-7	24.2	9.1	5.6	0.37	0.23	both
KUGSMM103	29.4	10.0	6.2	0.34	0.21	both

Adulomya uchimuraensis (Tanaka, 1960; Seki, 1983; Miyajima et al., 2014), but is clearly distinguishable from *A. uchimuraensis* in having smaller and higher shells (Figures 54 and 55). *Adulomya* sp. 1 resembles *A. chitanii* Kanehara, 1937 in shell size and outline (Figure 55), but can be distinguished from *A. chitanii* by the lacking of a pallial sinus.

DISCUSSION

Modern vesicomyid species diversity has been explained from the viewpoints of their bathymetric distribution (Fujikura et al., 2000), salinity or water temperature (Watanabe et al., 2013), and different preferences in hydrogen sulfide concentration at methane seeps (Barry et al., 1997; Sahling et al., 2002). On the other hand, little is known about the drivers of fossil vesicomyid species diversity. It is noteworthy that a total of four species, *Pliocardia*? *tanakai* new species, *Adulomya uchimuraensis*, *A. akanudaensis*, and *Adulomya* sp. 1, occur in a single formation. In particular, the former three species co-occur at the same seep carbonates, Akanuda and Anazawa limestones (Loc. 1). Such co-occurrence of more than two vesicomyid species seems to be rare in ancient seep environments. Although Kiel and Amano (2010) described three vesicomyid species, i.e., *Adulomya* sp. A, *Adulomya*? sp. B, and *Archivesica redwoodia* from a single site (USGS loc. 15399) in the lower Miocene Redwood Formation, Katalla District, southern Alaska, they are from a siliciclastic sedimentary rock without seep carbonates.

Modern analogues of such co-occurrence of two or more species at a single seep site have been recognized in Sagami Bay (Kojima and Ohta, 1997) and Monterey Bay (Barry et al., 1997). In Sagami Bay, two sibling species, *Archivesica soyoae* and *A. okutanii* (reassigned to the genus *Phreagena* by Krylova and Sahling, 2010) have different preferences in salinity and temperature (Watanabe et al., 2013). In Monterey Bay, *Archivesica kilmeri* (synonym of *soyoae*; Kojima et al., 2004; Okutani et al., 2009) and *Calyptogena pacifica* have different physiological tolerances to hydrogen sulfide concentrations (Barry and Kochevar, 1998), and these two species are segregated along sulfide gradients from the center to the margin of the seeps (Barry et al., 1997).

In the Bessho Formation, such segregation of the vesicomyid species at seeps could not be recognized unequivocally. In the large-sized seep limestones (Loc. 1), *Adulomya uchimuraensis* is dominant and ubiquitous throughout the carbonate bodies and even in the neighboring siltstone. Autochthonous specimens of *Pliocardia*? *tanakai* were found by one of the authors (TN) in the peripheral part of the Anazawa limestone (Loc. 1), which also contains scattered shells of *A. uchimuraensis*. Although the mode of fossil occurrence of *A. akanudaensis* at Loc. 1 is unknown, *A. akanudaensis* may be mixed with *A. uchimuraensis* in local shell concentrations as in the small-sized carbonate body at Loc. 3.

It is noted that the relative abundances of the three vesicomyid species are different between Locs. 1 and 3. In the large-sized seep carbonate bodies at Loc. 1, *Adulomya uchimuraensis* dominates throughout the carbonates (more than 200 specimens have been collected), whereas *Pliocardia*? *tanakai* (only total 10 specimens were obtained by K. Tanaka and the authors) and *A. akanudaensis* (only 9 specimens were collected by K. Tanaka) are rare. In the small-sized carbonate body at Loc. 3, *A. akanudaensis* (more than 30 specimens were collected by the authors) is as abundant as *A. uchimuraensis*, but *P.*? *tanakai* could not be found. The sizes of seep deposits are often related to longevity of fluid-flow history or fluid flux (Luff and Wallmann, 2003; Luff et al., 2004; Nesbitt et al., 2013), and the larger carbonate size at Loc. 1 suggests a longer fluid-flow history or a higher fluid flux than Loc. 3. This is also supported by the difference in the associated other molluscan fossils between these localities. While the seep carbonates at Loc. 1 contain diverse molluscan fossils including bathymodioline mussels, which are known from high-flux seeps (e.g., MacDonald et al., 1989; Olu et al., 1996), the carbonate at Loc. 3 contains less diverse mollusks. Moreover, the lithology and carbon isotopic compositions of the carbonates are also different between Locs. 1 and 3. The large seep carbonates at Loc. 1 consist of muddy micrite and calcite veins, showing low $\delta^{13}C$ values (−40 to −36‰; Sato et al., 1993), whereas the smaller carbonate body at Loc. 3 consists monotonously of micrite with $\delta^{13}C$ values ranging from −29.8 to +10.5‰. These suggest that the fluid intensity and composition, as well as longevity or flux, were different between the two seep sites (Peckmann et al., 2009; Kiel et al., 2014). Namely, an abundance of ^{13}C-depleted void-filling cements, such as sparitic veins in the carbonates at Loc. 1, is often attributed to a vigorous, advective flow, whereas the absence of such early-diagenetic cements suggests diffusive seepage (Peckmann et al., 2009; Kiel et al., 2014). The carbon isotopic compositions of seep carbonates are thought to vary depending on fluid composition such as thermogenic or biogenic methane (Whiticar, 1999) or crude oil (Roberts and Aharon, 1994), or on fluid flux. Therefore, different preferences in these factors relating to the seep activity may have been related to the relative abundance of the three vesicomyid species in the Bessho Formation.

Fluid flux probably also played a role in controlling the distribution of *Adulomya* sp. 1. This species is restricted to Loc. 2, where several cm-sized small carbonate concretions, having $\delta^{13}C$ values as low as −35‰, are scattered throughout the siltstone. Although the detailed study of this locality including carbon isotopic compositions of carbonates will be reported elsewhere, the scattered occurrence of small carbonate bodies suggests that the seepage was diffusive, with ephemeral and weak fluid flow (Nesbitt et al., 2013). In contrast, the larger seep carbonate bodies at Loc. 1 suggest longer fluid-flow history and a higher flow rate. The size difference between the seep deposits of Locs. 2 and 3 also suggests

some variation of seep activity, but it cannot be confirmed because most parts of the carbonate body at Loc. 3 originated from methanogenesis as well as methane oxidation.

In summary, the four fossil vesicomyid bivalves in the middle Miocene Bessho Formation may have had different preferences for fluid flux rates, fluid composition, and longevities among seep sites. The vesicomyid species diversity in this formation suggests that the diversification of vesicomyids through the Cenozoic could have been sustained not only by geographic and bathymetrical separation but also by adaptation to various seepage conditions.

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A new species of South Texas scrubsnail, *Praticolella* (von Martens, 1892) (Gastropoda: Polygyridae)

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ABSTRACT

The *Praticolella* of South Texas are highly visible and abundant snails with a confusing taxonomic history. In this paper, we provide 16S mitochondrial rDNA and morphological evidence to distinguish a new species of *Praticolella*, *Praticolella salina*, from southernmost coastal Texas. This native species previously was considered a distinct race of *P. griseola*, which we demonstrate does not occur natively in Texas.

Additional Keywords: mtDNA, *Praticolella griseola*, *Praticolella mexicana*, Cameron County, Texas

INTRODUCTION

Praticolella (von Martens, 1892) are small (7–15 mm wide), globose, helicoid land snails found in open, grassy habitats. Two species in this genus, *P. griseola* (Pfeiffer, 1841) and *P. mexicana* Perez, 2011, have established populations worldwide via human-mediated transport (Robinson 1999, Perez 2011). *Praticolella* sensu stricto contains ten currently recognized species that occur in Texas. Six species are found in the Rio Grande Valley of South Texas, including four native and two non-native species of *Praticolella*. The South Texas *Praticolella* have a great deal of overlap in habitat, shell shape, color, aperture shape, and shell banding patterns; indeed, this region has been called a "great melting pot" for these snails (Cheatum and Fullington, 1971).

Over the last 150+ years, previous workers have recognized a unique population of *Praticolella* located in coastal South Texas, referring to it as a unique "race" of *P. griseola* (e.g. Orcutt, 1915; Rehder, 1966). In 2011, Perez described *Praticolella mexicana* and distinguished this species occurring in Texas from *P. griseola* and *P. berlandieriana* (Moricand, 1833). Phylogenetic work by Perez (2011) based on mtDNA sequences established that a few individuals identified as *P. griseola* from Cameron County Texas formed a distinct clade; with only a single population represented in that study, that author declined to establish a formal distinctive taxonomic status for that population. This population was also found to be distinct using geometric morphometrics (Perez, 2011). In the present study, we sampled additional populations of *Praticolella* from coastal Cameron County, Texas, and used anatomical and genetic data to determine that these populations represented a previously unrecognized, distinct species.

MATERIALS AND METHODS

Collections and Molecular Methods: Representatives of the populations in Cameron County were collected by hand and individuals were frozen at −20°C prior to DNA extraction. We amplified the mitochondrial 16S rDNA gene of twenty individuals from four of these populations (Figure 1, Table 1) using the degenerate 16sar-deg and 16sbr-deg primers described in Perez (2011). Methods for DNA extraction and PCR also follow Perez (2011), and Sanger sequencing was carried out by Beckman Coulter Genomics. Contigs were assembled in SeqMan Pro (DNASTAR 2014. SeqMan Pro®. Madison, WI) and added to the sequences used in Perez (2011). The dataset was aligned using MUSCLE 3.7 (Edgar, 2004) followed by elimination of poorly aligned positions in Gblocks 0.91b (Castresana 2000) implemented at Phylogeny.fr (Dereeper et al. 2008) (http://phylogeny.lirmm.fr/phylo_cgi/index.cgi). We used jModeltest (2.1.7) (Guindon and Gascuel, 2003; Darriba, et al. 2012) to select TIM1+I+G (Posada 2003) as the best model for our data. Maximum likelihood analysis and 1000 bootstrap replicates were carried out in Garli 2.01 (Zwickl, 2006). Base frequencies and substitution rate categories were estimated from the data.

Species Delimitation Analyses: We used three methods to assess whether our labeled clades represented

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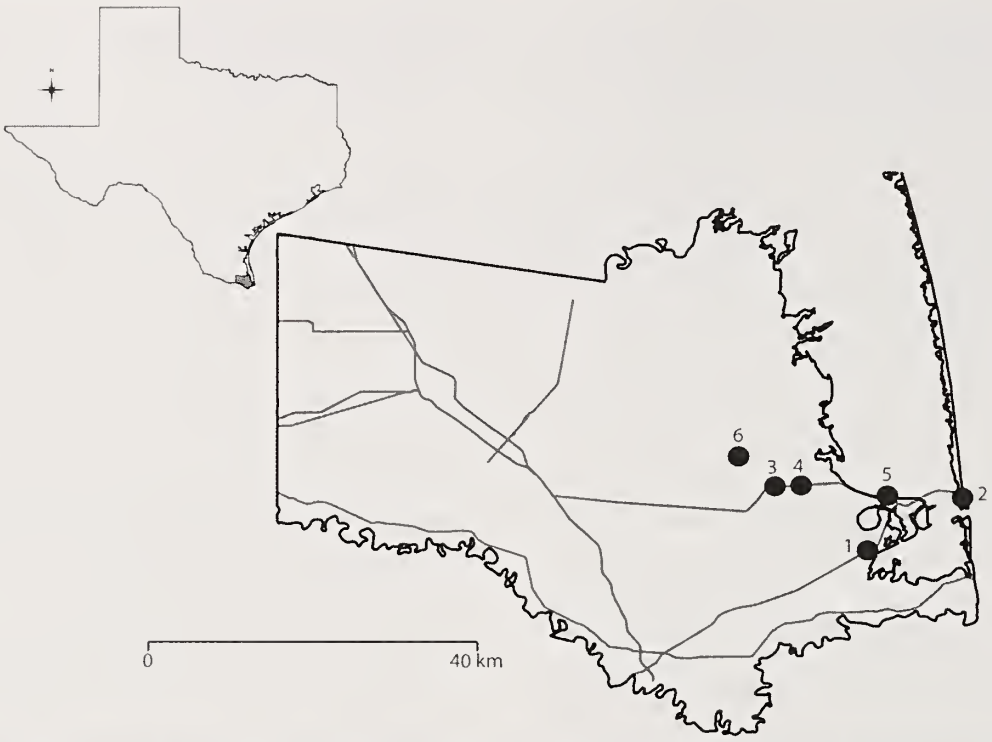

Figure 1. Map with sampling sites for Cameron County populations included in the molecular and soil analyses (Table 1 and Figure 2). The location of Cameron County Texas is depicted in gray in the inset map. State highways are shown as gray lines in the Cameron County map.

species under the phylogenetic species concept (PSC). Under the PSC, species are both the smallest units for which phylogenetic relationships can be reliably inferred (Baum and Shaw, 1995) and entities residing at the transition between evolutionary relationships that are best reflected as reticulate genealogical connections (Goldstein et al., 2000). With the Species Delimitation Plugin (SDP) (Masters et al., 2011) in Geneious 8 (Biomatters Ltd., Kearse et al., 2012), we calculated Rosenberg's $P_{(AB)}$ to test the reciprocal monophyly of each labeled clade and its closest clade (Rosenberg, 2007). Rejection of the null hypothesis suggests genealogical separation of distinct taxa versus monophyly arising randomly according to a Yule model. Significance was determined following Rosenberg (2007). The SDP also assessed the probability of assigning a given individual to its member clade in two ways (Ross et al., 2008). A strict probability was determined for placing an individual into the correct clade while not placing it into the sister clade, and a liberal probability was calculated for placing an individual into either the correct clade or sister clade (Masters et al., 2011). We also calculated the genealogical sorting index (GSI) for each labeled clade in our phylogeny. The GSI statistic quantifies the degree of exclusive ancestry for identified groups in a rooted tree and tests whether it is greater or less than that expected by chance. Significant results suggest that *a priori* groups do not represent a single mixed genealogical ancestry. We employed a GSI web service (http://molecularevolution.org/software/phylogenetics/gsi/) and assessed significance at α=0.05 using 10,000 tip label permutations on our fixed topology. Finally, we used the Poisson tree processes (PTP) model (Zhang et al., 2013) to assess whether the number of substitutions between our labeled clades was significantly higher than that within those same clades; significantly more substitutions between clades implies that they represent separate phylogenetic species. This method does not require an ultrametric phylogeny nor an evolutionary time context. We used an online likelihood implementation of PTP (http://species.h-its.org/ptp/) with default settings.

Morphological Examination: We collected five measurements from each of 42 individuals, measured to the nearest 0.1 mm with digital calipers: maximum shell height parallel to the axis of coiling, maximum shell width perpendicular to the axis of coiling, maximum aperture width, aperture height perpendicular to aperture width measurement, and maximum umbilicus diameter. Only adult specimens with complete reflected lips were measured. The number of whorls was estimated using the method described by Cheatum and Fullington (1971: 15, fig. 1c) to the nearest 0.25 of a whorl at 20× magnification. This method counts each whorl as a complete spiral turn of the shell. A stacked composite image of the holotype shell was assembled using Helicon Focus 6.7.1 (Helicon Soft Limited). To relax snails for dissection, snails were drowned in room temperature water for 30 minutes, followed by incubation for 90 minutes at 37°C (Kruckenhauser et al., 2011). Following relaxation snails were preserved in 70% ethanol until dissection. Soft tissues

Table 1. Locality and collection information for populations examined in this study for molecular analysis, soil analysis, and additional material examined. #Included from Perez 2011. *At this site only dry shells of *P. salina* were present. Specimens are deposited at the Academy of Natural Sciences of Philadelphia Drexler University (ANSP). ANSP numbers beginning with "A" are lots preserved in alcohol. Field Museum of Natural History accession is coded FMNH. Latitude and longitude presented in decimal degrees. Cameron County Population Numbers are those labeled on Figure 1.

Species	Cameron County Population Number	Collection information	Museum Numbers	Lat.	Long.
Records for Molecular Analyses					
Praticolella salina	1	8 km S of Port Isabel, Highway 48, Entrance to Laguna Atascosa National Wildlife Refuge, Cameron Co., Texas, K.E. Perez, E. Ruiz, 8 Nov 2014. Type locality.	ANSP A24736 (Holotype), ANSP 467509 (Paratypes), ANSP A24737	25.9957	−97.311
Praticolella salina	2	University of Texas Rio Grande Valley Coastal Studies Lab, Isla Blanca Park, S end of South Padre Island, Cameron Co., Texas, K.E. Perez, D. Deshommes, 19 Oct 2014.	ANSP 467487, A24735	26.0755	−97.159
Praticolella salina	3	2.5 km W of the water treatment facility at Laguna Vista. S side of Highway 100, Cameron Co., Texas, K.E. Perez, D. Deshommes, 19 Oct 2014.	ANSP 467486, A24734	26.0903	−97.348
Praticolella salina	4	1 km W of Laguna Vista, S side of Highway 100, Cameron Co., Texas, K.E. Perez, E. Ruiz, 8 Nov 2014.	ANSP-A 24738	26.0904	−97.349
Praticolella salina (called "*P. griseola* Cameron Co." in Perez 2011)	5#	Port Isabel High School on N (bay side) of Park Road 1, Port Isabel, Cameron Co., Texas, T. Glenn Littleton and N.E. Strenth, 18 Dec 1990.	ANSP-A 22074, ANSP 426021	26.077	−97.227
Additional location for soil analysis					
Praticolella salina	6*	Bayview, Cameron Co. Texas, Toronja Dr., 100 m from Farm-to-Market Road 2480, K.E. Perez, E. Ruiz, 8 Jul 2015.	ANSP 456531	26.119604	−97.400126
Additional Material Examined					
Praticolella salina		2.5 km W of the water treatment facility at Laguna Vista, S side of Highway 100, Cameron Co., Texas, K.E. Perez, E. Ruiz, 8 Jul 2015.	ANSP 456530, A24738	26.0903	−97.348
Praticolella salina		Bayview, Cameron Co., Texas, Toronja Dr., 100 m from Farm-to-Market Road 2480, K.E. Perez, E. Ruiz, 8 Jul 2015.	ANSP 456531	26.119604	−97.400126
Praticolella salina		2.5 km W of Laguna Vista on S. side of Highway 100, Cameron Co., Texas, E. Ruiz, 29 Mar 2016.	ANSP 456532, A24739	26.0903	−97.348
Praticolella salina		8 km S of Port Isabel, Highway 48, Entrance to Laguna Atascosa National Wildlife Refuge, Cameron Co., Texas, K.E. Perez, E. Ruiz, 8 Jul 2015.	ANSP 467533	25.9957	−97.311
Praticolella salina		14.5 km W of Boca Chica, Brady Unit, Laguna Atascosa National Wildlife Refuge, off HWY 4, Cameron Co., Texas, K.E. Perez, E. Ruiz, 30 Oct 2014.	ANSP 467534	25.9621	−97.27893
Praticolella mexicana		Mcallen, TX, 600 N. 7th St., backyard, Hidalgo Co., Texas, K.E. Perez, 4 Aug 2015.	ANSP A24740	26.2085	−98.2255
Praticolella salina (labeled as *P. griseola*)		Port Brownsville, Cameron Co., Texas, L. Hubricht, 9 Sep 1954.	FMNH 259156	25.9509	−97.4109

were removed from the shell and a mid-sagittal incision was used to expose the internal anatomy. Connective tissue was removed followed by separation of the genitalia. All structures were photographed in water.

Soil Sampling: To determine the soil salinity in the habitat of this species, soil samples were collected at four of the collection localities for live snails from Cameron County (Sites 1, 2, 3, and 5 from Table 1). Small samples of soil were collected by a gloved hand covering the entire local extent of the population into a single, 5 L collection. These samples were mixed in a plastic bucket and a subsample was sent to the University of Louisiana at Monroe Environmental Analysis Laboratory for quantification of all extractable elements. Soil descriptors followed Soil Survey Division Staff (1993).

RESULTS

Twenty new 16S sequences (GenBank KX431997–KX432016) from four populations of the new species *P. salina* were generated. Maximum likelihood analysis of 436 bp of 16S mt sequences of 110 individuals of nine putative species of *Praticolella* yielded a single tree (log likelihood = −4465.5927; Figure 2) with an overall tree topology similar to that found by Perez (2011). Outgroups included in the analysis were representatives of the other genera of Polygyrini included in Perez (2011): *Lobosculum pustuloides* (Bland, 1858); *Polygyra septemvolva* Say, 1818; *Polygyra cereolus* (Mühlfeld, 1816); *Daedalochila hippocrepis* (Pfeiffer, 1848); *Linisa texasiana* (Moricand, 1833); and *Millerelix mooreana* (W.G. Binney, 1858). Species-level clades were well supported but relationships among these taxa had little bootstrap support. Two putative species-level clades (monophyletic groups identified by the species delimitation analyses conducted) we recognized currently lack names: an unnamed species from Soto de la Marina, Tamaulipas, Mexico, herein referred to as "Soto"; and an unnamed species from an introduced (greenhouse) population in Florida, USA, herein referred to as "Florida". Three other nominal species (*P. taeniata* Pilsbry, 1940; *P. pachyloma* (Menke in Pfeiffer, 1847); and *P. candida* Hubricht, 1983) appeared to form a single species-level clade from South Texas, referred to herein as the "South Texas Clade". A weakly supported clade (54%) suggested a close relationship between *P. salina* and the Florida population. The *P. salina* clade had some internal population-level molecular structuring with individuals from each population appearing in the various shallow clades with the exception of the South Padre Island individuals which are separate.

We tested our nine labeled species-level clades (Figure 2) using three species delineation methods. Based on Rosenberg's $P_{(AB)}$, the SDP supported recognition of seven of our nine labeled clades as reciprocally monophyletic taxonomic entities (Table 2 and Figure 2). The *Praticolella berlanderiana* clade and South Texas Clade had non-significant $P_{(AB)}$ values. Probabilities of assigning individuals to their correct clades varied from 59–95% under the "strict" method and 87–99% under the "liberal" method. The clade representing the new species had probabilities of 92% and 99% under the "strict" and "liberal" criteria respectively. All nine labeled clades possessed significant GSI values ($p<0.05$), suggesting no evidence of mixed ancestry in any group. The maximum likelihood PTP solution identified six of our labeled clades as possible phylogenetic species: *P. berlandieriana*; *P. trimatris*; South Texas Clade; Soto; Florida; and *P. salina*. These species were supported by all three species delineation methods, however, *P. mexicana*, *P. griseola*, and *P. flavescens* were not supported by PTP, perhaps because of unequal sampling or unrecognized diversity in these clades.

Soils at Site 1 (type locality) had a pH of 7.67, a salinity of 11.6 parts per thousand (ppt), and contained 0.89% organic matter. Across all sites, pH ranged from 7.13 to 8.33, salinity from 0.42 to 22.9 ppt, and organic matter from 0.13% to 1.59%. This indicated that *P. salina* was collected in areas with neutral to moderately alkaline mineral soils. The salt marsh sites (sites 1 and 3) were considered highly saline, while the dune (site 2) and agricultural (site 6) sites were considered non-saline.

SYSTEMATICS

Class Gastropoda Cuvier, 1791
Family Polygyridae Pilsbry, 1930

Genus *Praticolella* von Martens, 1892

Dorcasia Binney, 1878: 356.
Praticola Strebel and Pfeiffer, 1880: 38 [*non* Swainson, 1837]
Praticolella von Martens, 1892: 138.

Type Species: *Praticola ocampi* Strebel and Pfeiffer, 1880 (= *Helix ampla* Pfeiffer, 1866)

Praticolella salina new species Perez and Ruiz, 2017

(Figures 4–11)

Helix griseola Pfeiffer, 1841.—Binney, 1857: pl. 49 fig. 2, pl. 72 fig. 20.
Praticolella griseola (Pfeiffer, 1841).—Pilsbry, 1940: 690 (misidentification in part), fig. 425; Webb, 1951: 140, pl. 48 fig. 30; Rehder, 1966: 290–291 (misidentification in part), fig. 20; Cheatum and Fullington, 1971: 38–39 (misidentification in part), figs. 2, 12. Neck, 1977: 1–4 (misidentification in part).

Diagnosis: Peristome reflected without inner thickening and narrow throughout, unique among Texas *Praticolella*; lower surface of body whorl brown with a single to several white bands; shell wider than high.

Description: Shell large for *Praticolella*, narrowly umbilicate, depressed, brown with white pigmented stripes. Peristome mostly white, barely reflected at parietal wall but heavily reflected at umbilicus, partially obstructing

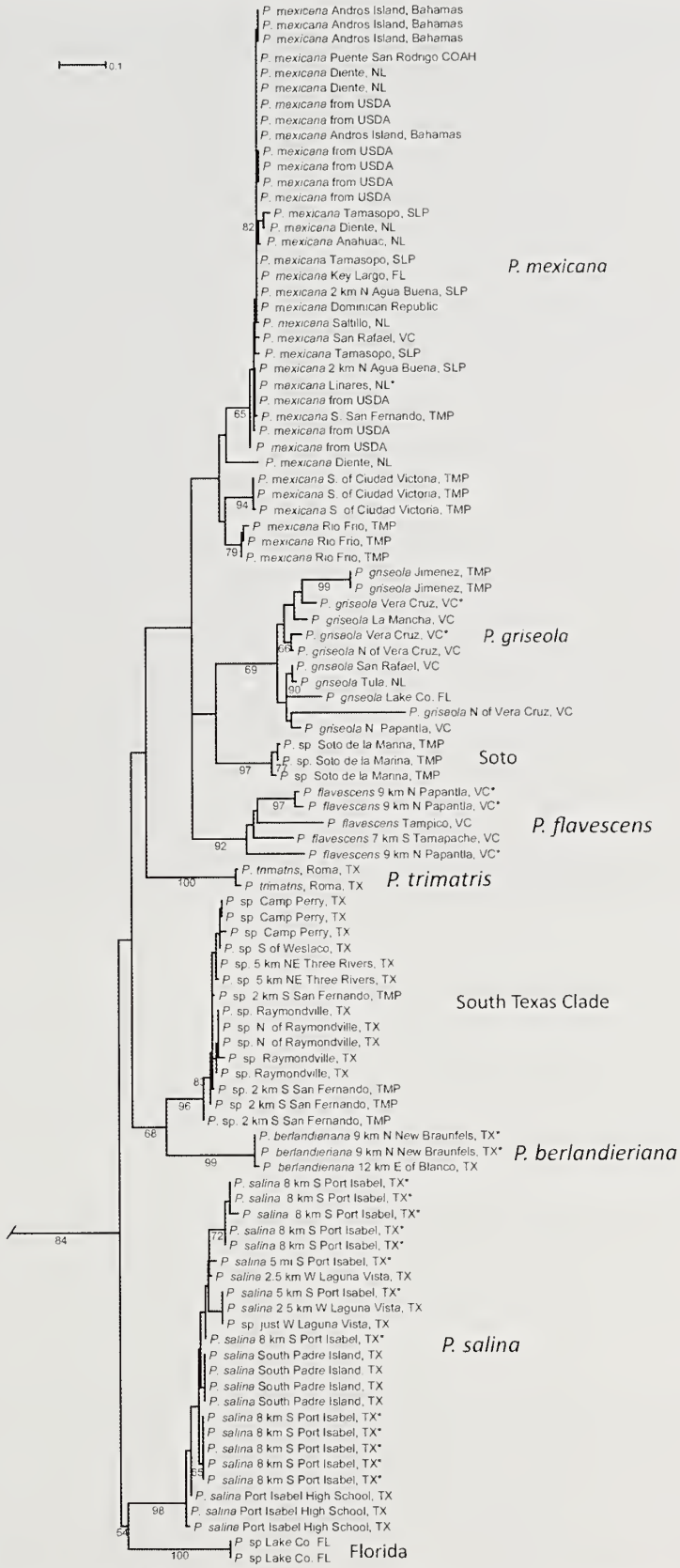
0.1
P. mexicana Andros Island, Bahamas
P. mexicana Andros Island, Bahamas
P. mexicana Andros Island, Bahamas
P. mexicana Puente San Rodrigo COAH
P. mexicana Diente, NL
P. mexicana Diente, NL
P. mexicana from USDA
P. mexicana from USDA
P. mexicana Andros Island, Bahamas
P. mexicana from USDA
P. mexicana from USDA
P. mexicana from USDA
P. mexicana from USDA
P. mexicana Tamasopo, SLP
P. mexicana Diente, NL
P. mexicana Anahuac, NL
P. mexicana Tamasopo, SLP
P. mexicana Key Largo, FL
P. mexicana 2 km N Agua Buena, SLP
P. mexicana Dominican Republic
P. mexicana Saltillo, NL
P. mexicana San Rafael, VC
P. mexicana Tamasopo, SLP
P. mexicana 2 km N Agua Buena, SLP
P. mexicana Linares, NL*
P. mexicana from USDA
P. mexicana S. San Fernando, TMP
P. mexicana from USDA
P. mexicana from USDA
P. mexicana Diente, NL
P. mexicana S. of Ciudad Victoria, TMP
P. mexicana S. of Ciudad Victoria, TMP
P. mexicana S. of Ciudad Victoria, TMP
P. mexicana Rio Frio, TMP
P. mexicana Rio Frio, TMP
P. mexicana Rio Frio, TMP
P. griseola Jimenez, TMP
P. griseola Jimenez, TMP
P. griseola Vera Cruz, VC*
P. griseola La Mancha, VC
P. griseola Vera Cruz, VC*
P. griseola N of Vera Cruz, VC
P. griseola San Rafael, VC
P. griseola Tula, NL
P. griseola Lake Co. FL
P. griseola N of Vera Cruz, VC
P. griseola N. Papantla, VC
P. sp. Soto de la Marina, TMP
P. sp. Soto de la Marina, TMP
P. sp. Soto de la Marina, TMP
P. flavescens 9 km N Papantla, VC*
P. flavescens 9 km N Papantla, VC*
P. flavescens Tampico, VC
P. flavescens 7 km S Tamapache, VC
P. flavescens 9 km N Papantla, VC*
P. trimatris, Roma, TX
P. trimatris, Roma, TX
P. sp. Camp Perry, TX
P. sp. Camp Perry, TX
P. sp. Camp Perry, TX
P. sp. S of Weslaco, TX
P. sp. 5 km NE Three Rivers, TX
P. sp. 5 km NE Three Rivers, TX
P. sp. 2 km S San Fernando, TMP
P. sp. Raymondville, TX
P. sp. N. of Raymondville, TX
P. sp. N. of Raymondville, TX
P. sp. Raymondville, TX
P. sp. Raymondville, TX
P. sp. 2 km S San Fernando, TMP
P. sp. 2 km S San Fernando, TMP
P. sp. 2 km S San Fernando, TMP
P. berlandieriana 9 km N New Braunfels, TX*
P. berlandieriana 9 km N New Braunfels, TX*
P. berlandieriana 12 km E of Blanco, TX
P. salina 8 km S Port Isabel, TX*
P. salina 8 km S Port Isabel, TX*
P. salina 8 km S Port Isabel, TX*
P. salina 8 km S Port Isabel, TX*
P. salina 8 km S Port Isabel, TX*
P. salina 5 mi S Port Isabel, TX*
P. salina 2.5 km W Laguna Vista, TX
P. salina 5 km S Port Isabel, TX*
P. salina 2.5 km W Laguna Vista, TX
P. sp. just W Laguna Vista, TX
P. salina 8 km S Port Isabel, TX*
P. salina South Padre Island, TX
P. salina South Padre Island, TX
P. salina South Padre Island, TX
P. salina South Padre Island, TX
P. salina 8 km S Port Isabel, TX*
P. salina 8 km S Port Isabel, TX*
P. salina 8 km S Port Isabel, TX*
P. salina 8 km S Port Isabel, TX*
P. salina 8 km S Port Isabel, TX*
P. salina Port Isabel High School, TX
P. salina Port Isabel High School, TX
P. salina Port Isabel High School, TX
P. sp Lake Co. FL
P. sp Lake Co. FL
P. mexicana
P. griseola
Soto
P. flavescens
P. trimatris
South Texas Clade
P. berlandieriana
P. salina
Florida

Figure 2. Maximum likelihood phylogeny based on 436 bp of 16S mt sequences of 110 individuals. Only *Praticolella* sensu stricto are shown. Bootstrap values >50% shown below the nodes. Individuals marked with * were collected from type locality. Outgroups are omitted from the figured tree.

Table 2. Results from the Species Delimitation Plugin analysis. Clades correspond to those in Figure 2. Ps and Pl are probabilities of correct identification under strict and liberal criteria respectively. Asterisks (*) signify significant values of Rosenberg's $P_{(AB)}$ and thus separate taxonomic entities by that measure. Clades with significant GSI values and identified as possible phylogenetic species by PTP are also indicated.

Labeled Clade	Ps	Pl	$P_{(AB)}$	GSI	PTP
P. salina	0.92	0.97	2.7×10^{-4} *	yes	yes
Florida	0.59	0.98	2.7×10^{-4} *	yes	yes
South Texas Clade	0.95	0.99	1.4×10^{-4}	yes	yes
P. berlandieriana	0.78	0.99	1.4×10^{-4}	yes	yes
P. trimatris	0.58	0.97	4.5×10^{-5} *	yes	yes
P. mexicana	0.94	0.98	1.0×10^{-28} *	yes	no
Soto	0.77	0.99	4.2×10^{-4} *	yes	yes
P. griseola	0.74	0.92	4.2×10^{-4} *	yes	no
P. flavescens	0.61	0.87	2.6×10^{-10} *	yes	no

umbilicus in most individuals. Aperture slightly lunate with light parietal callus. Suture smooth but uneven where intersected by growth lines. Protoconch smooth, with longitudinal growth lines (radial lines) appearing by the second spire whorl. Spire and body whorls white above a single translucent, light-brown band around the periphery; up to six additional white stripes below that translucent band. Umbilicus outlined by a single translucent, light-brown band often followed by a white pigmented band. Mean shell height 9.10 ± 0.48 mm, width 12.21 ± 0.68 mm, height/width ratio 0.75; mean aperture height 6.4 2± 0.66 mm, width 6.42 ± 0.14 and height/width ratio 0.88 (Table 3).

Body color brown in life. Largest branch of divided penial retractor muscle inserted on apex of penis. Two smaller branches attached to penis with vas deferens passing between them (Figure 3). Vas deferens of consistent diameter across its length. Penis bipartite with one smooth bulb and distinct appendix. Penial appendix, in the unextended state, slightly narrower at penial attachment, widening and becoming bulbous, about one-half total penial width. Distal end of the penial appendix slightly hooked. Epiphallus noticeably smaller in diameter than the penis, with the vas deferens at the terminal end; flagellum absent. Bursa copulatrix thin, clavate, widening slightly at the terminus. Ovotestis appears as a sponge-like, irregular mass.

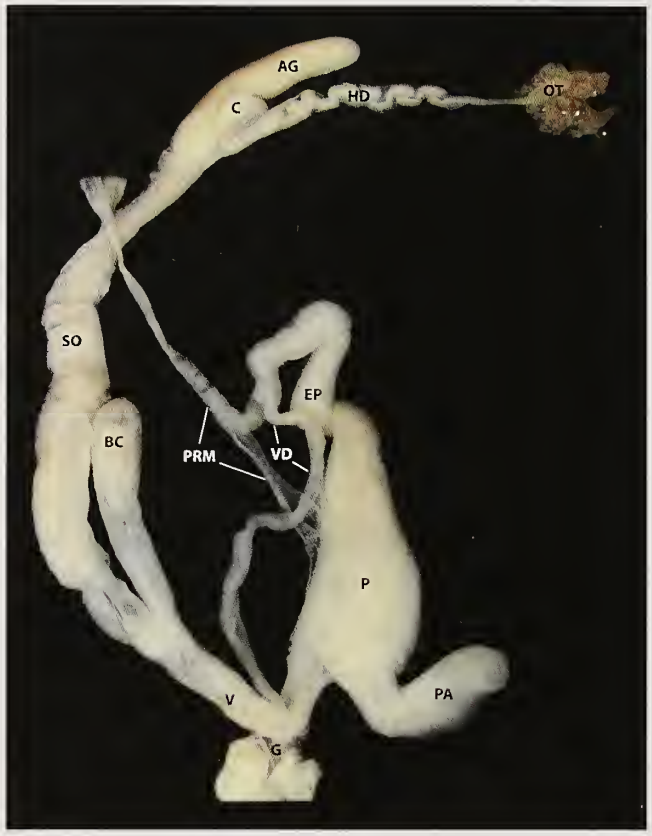

Figure 3. Internal anatomy of specimen from Cameron County, TX. ANSP A24739. AG, albumen gland; BC, bursa copulatrix; C, carrefour (spermatheca and fertilization pouch complex); EP, epiphallus; G, genital pore; HD, hermaphroditic duct; OT, ovotestis; P, penis; PA, penial appendix; PRM, penial retractor muscle; SO, spermoviduct; V, vagina; VD, vas deferens.

Type Material: Holotype, ANSP A24736; Paratypes, ANSP 467509 (35 individuals), all from type locality.

Type Locality: 8 km south of Port Isabel on HWY 48, Laguna Atascosa National Wildlife Refuge, Cameron County, TX. 25.9957 N, −97.311 W, (8 November 2014, coll. K. E. Perez and E. Ruiz).

Distribution and Habitat: Vegetated dunes and sands and clay soils on South Padre Island and coastal Cameron County, Texas. These locales are associated with Gulf Coast saline prairie habitats in the South Texas Lomas

Table 3. Shell measurements for the *Praticolella* species under consideration. Only adult shells with a full lip were measured. Measurements for *P. griseola* (n=36) are from (Perez 2011) and *P. salina* (n=42) from the present study. Values present are the range of values, mean, and standard deviation. Measurements taken: shell height (h), width (w), aperture height (aph), aperture width (apw), umbilicus width (umb), and number of whorls (# of whorls).

Species	h (mm)	w (mm)	aph (mm)	apw (mm)	umb (mm)	# of whorls
P. griseola	8.32–11.29	5.8–7.92	4.4–6.7	4.16–5.75	0.38–1.03	4.75–5.5
	9.65±0.78	6.91±0.51	5.34±0.47	4.88±0.39	0.71±0.16	5.12±0.16
P. salina	8.04–10.28	10.84–13.55	4.65–6.71	5.17–7.84	0.39–0.97	5–5.75
	9.10±0.48	12.21±0.68	5.63±0.50	6.42±0.66	0.65±0.14	5.39±0.18

Figures 4–11. Shells of *Praticolella salina* new species. **4–8.** Holotype, ANSP A24736, from type locality: 8 km S of Port Isabel on HW 48, Laguna Atascosa National Wildlife Refuge, Cameron County, Texas, 8 Nov 2014, K.E. Perez, E. Ruiz, lateral, basal, and apical views of the shell, close up of suture and embryonic whorls, w=13.60 mm, h=10.03 mm, 5.5 whorls. **9.** ANSP 467487; UTRGV Coastal Studies Lab, Isla Blanca Park, south end of South Padre Island, Cameron County, Texas, 19 Oct 2014. K.E. Perez, D. Deshommes, w=10.06 mm, h=7.64 mm, 5.0 whorls. **10.** ANSP 467487; UTRGV Coastal Studies Lab, Isla Blanca Park, south end of South Padre Island, Cameron County, Texas, 19 Oct 2014. K.E. Perez, D. Deshommes, w=10.88 mm, h=8.59 mm, 5.5 whorls. **11.** ANSP A24739, 2.5 km W of the water treatment facility at Laguna Vista, S side of HWY 100, Cameron County, Texas, 29 March 2016, E. Ruiz, w=11.87 mm, h=9.23 mm, 5.25 whorls.

ecological system (Natureserve, 2016), a rare plant community recognized by Texas Parks & Wildlife. Individuals have been found in Dune sand, Harlingen clay, Point Isabel clay, Lomalto clay, and Laredo silty clay loam soil types. Dominant vegetation in the clay soils includes shoregrass (*Monanthochloe littoralis*), bushy seaside tansy (*Borrichia frutescens*), and Florida / gutta-percha Mayten (*Maytenus phyllanthoides*); all are salt tolerant species. Snails were found crawling or estivating on cactus (*Opuntia* sp.) at Sites 1–4, Site 5 was recently modified to citrus orchards and cornfields, with no cactus present. This species appears to have a very limited distribution that is likely reduced from its previous extent. We find only dry shells of *P. salina* farther inland and in close proximity to extant *P. mexicana* colonies. The species likely extends into coastal, northern Tamaulipas, Mexico as well, but that area has not been sampled by the authors.

Etymology: From Latin, *salinus*, salty (derivative of *sal*), in reference to the species' unusual occurrence in highly saline terrestrial habitats.

Comparisons with Other *Praticolella*: The shell of *P. salina* is distinct from that of *P. griseola* in being larger, wider and less globose, and lacking a diagnostic cinnamon-brown pigmented band. The aperture of *P. salina* is also wider than high compared to the nearly round aperture of *P. griseola*. *Praticolella salina* can be distinguished from shells of the South Texas *Praticolella* clade members by its thin versus thickened and deeply reflected peristome. It can be distinguished from *P. mexicana* in always

possessing some white pigmented bands that follow the axis of coiling; none of them, however, run against the axis of coiling or have a pattern of alternating white, pigmented and brown, unpigmented, broken "rays" running perpendicular to the axis of coiling as is often the case in *P. mexicana*.

The penial appendix of *P. salina* is distinctive as it is distally clavate, hooked, and about half the width of the penis. In *P. mexicana*, this structure is equally wide along its length, lacks any hook, and is slightly less than the penile width. The bursa copulatrix of *P. salina* is clavate, only slightly wider at the distal end than at the insertion into the vagina. This structure is distinguishable from that of the South Texas clade which is reniform (Vanatta, 1915), and from both *P. mexicana* and *P. berlandieriana* (Webb, 1967), which have expanded spatulate distal ends that taper to narrow insertion points.

Remarks: Perez (2011) reviewed the turbulent taxonomic history of *Praticolella* from southern Texas and northern Mexico, especially as it relates to nominal *P. griseola* from Cameron County, Texas. *Praticolella griseola* was originally described from Veracruz, Mexico, by Pfeiffer (1841). Orcutt (1915) first considered *P. griseola* of Texas to be distinct instead of an example of a polymorphic species. Pilsbry (1940) figured *P. salina* from Brownsville, Texas, as *P. griseola* and noted that Brownsville specimens were larger and banded differently than the type specimen. Rehder (1966) compared *P. griseola* from throughout its range and considered the Brownsville population to be a distinct race, characterized by large specimens with sharply defined color bands. In their review of Texas *Praticolella*, Cheatum and Fullington (1971) reviewed *P. griseola*. The descriptions, distribution, and measurements given by Cheatum and Fullington for that latter species represent *P. salina* as well as other South Texas species. Neck (1977) revised nomenclatural and distribution records for *P. griseola* of previous authors, and restricted *P. griseola* in Texas to Cameron County near Brownsville and Laguna Atascosa National Wildlife Refuge. Herein we consider all of these treatments of *P. griseola* in South Texas to be consistent with and indicative of *P. salina*.

By restricting its distribution to southern Texas (possibly south to Tamaulipas), we aim to emphasize the separation of *Praticolella salina* and *P. griseola* evidenced by morphological and molecular data. *Praticolella griseola* sensu stricto is a species from the Gulf Coastal Plain of south-central Mexico that has been moved through human activity with established populations in Alabama, Florida, and Louisiana. Any occurrence of true *P. griseola* in Texas is therefore considered an introduction, not a native and/or remnant population. Additional historical records of *P. griseola* in Texas have been or should be reassigned to other species, including *P. mexicana*. As such, we have limited our synonymy to those works that clearly illustrated a shell we consider to be *P. salina*. Other works listing *P. griseola* ambiguously from Texas may represent *P. salina*, but without additional evidence they were excluded.

We often find *Praticolella salina* occurring with other *Praticolella* species. In Brownsville, for example, we confirmed Pilsbry's (1940) observation that it occurs with *P. taeniata*. Similarly, we have also found *P. salina* within a few meters of *P. mexicana*, where the former was in native habitat and the latter in the grassy verge of a roadway. This is reminiscent of how other *Praticolella* species co-occur, such as *P. griseola* and *P. flavescens* in central Mexico.

The present study with extensive sampling in Cameron County found only eight populations of *Praticolella salina* (seven with living individuals present) in a coastal region with rapid habitat modification due to housing and business developments. This finding is typical of land snails, one of the most diverse, relatively poorly known, and imperiled groups of animals globally (Lydeard et al., 2004).

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A new genus and species of Neomphalidae from a hydrothermal vent of the Manus Back-Arc Basin, western Pacific (Gastropoda: Neomphalina)

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ABSTRACT

Lamellomphalus manusensis new genus, new species is described from a hydrothermal vent site of the Manus Back-Arc Basin. The familial assignment is based on morphologies of shell and external anatomy. The new taxon is superficially similar to some members of Peltospiridae McLean, 1989 in general shell shape, but differs from all peltospirids in having sex dimorphism and presence of a copulatory organ. *Lamellomphalus manusensis* is characterized by possessing haliotiform shell with some degree of coiling, which could be considered as an intermediate form in the family Neomphalidae McLean, 1981, between species with regularly coiled shells (*Cyathermia* Warén and Bouchet, 1989; *Lacunoides* Warén and Bouchet, 1989; *Planorbidella* Warén and Bouchet, 1993, and *Solutigyra* Warén and Bouchet, 1989) and limpet-like shells (*Neomphalus* McLean, 1981 and *Symmetromphalus* McLean, 1990). This feature thus distinguishes the new taxon from other neomphalids. A phylogenetic reconstruction based on cytochrome *c* oxidase I gene (COI) also supports its placement within Neomphalidae.

Additional keywords: Gastropoda, Neomphaloidea, chemosynthetic environment, new taxon

INTRODUCTION

The Manus Back-Arc Basin is of particular biological interest due to its location between the biologically well studied Mariana Trough and the vent communities of the North Fiji and Lau Back-Arc Basins. That special geographical environment yields many interesting and new gastropods, attracting the interest of many scientists (e.g. Desbruyères and Laubier, 1989; Beck, 1991, 1992a, 1992b, 1993; Bouchet and Warén, 1991; Warén and Bouchet, 1993).

Neomphalina (Warén and Bouchet, 1993) are a group of gastropods that inhabits chemosynthetic environments (Desbruyères et al., 2006; Sasaki et al., 2010) and sunken wood (Hess et al., 2008). Among them, Neomphalidae is a particular family that by far is consisting of six genera and eight species, known from East Pacific Rise (Warén and Bouchet, 1989), Galapagos Rift (McLean, 1981; Warén and Bouchet, 1989), Lau Basin (Warén and Bouchet, 1993), Axial Seamount (Warén and Bouchet, 2001) and Mariana Back-Arc Basin (McLean, 1990).

In June 2015, during a scientific investigation carried out by the Institute of Oceanology, Chinese Academy of Sciences (IOCAS), several limpet-shaped gastropods were collected in the Manus Back-Arc Basin by a dive of the ROV Faxian (based on mother ship R/V Kexue). Observations on their shell, radula features and external anatomy confirmed that they represent a new genus and a new species belonging to the family Neomphalidae McLean, 1981. In present study, we describe and illustrate this new taxon, comparing it to its closest relatives.

MATERIALS AND METHODS

More than 130 specimens were collected during single dive of the ROV Faxian (IOCAS) in June, 2015, at a hydrothermal vent site in the Manus Back-Arc Basin. This vent field is composed of both fissure areas and more active zones with small anhydrite and tall sulfide and silica chimneys ejecting greyish-black fluids (see Fourre et al., 2006 for details). The entire area is partially colonized by vestimentiferan worms (Siboglinidae) associated with the large gastropods *Ifremeria nautilei* Bouchet and Warén, 1991, mussels, shrimps and galatheid crabs.

The specimens described herein were collected by the mechanical arm of the ROV Faxian in the course of sampling the rock where specimens were attached. The materials were fixed in 99.5% ethanol directly after collection. Preserved specimens were brought to Marine

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Table 1. Shell measurements of *Lamellomphalus manusensis* new species.

Measurements (mm)	Shell		
	Length	Width	Height
Lamellomphalus manusensis			
Holotype (MBM283053)	8.8	5.7	2.9
Paratype (MBM283054)	6.6	4.7	2.7
Range	3.5–8.9	2.5–6.5	1.5–3.3
Mean	5.9	4.4	2.6

Biological Museum, Chinese Academy of Sciences (MBMCAS), for further study. Shell measurements were taken with a caliper with accuracy of 0.1 mm (see Table 1).

Scanning Electron (SEM) and Light Microscopies (SEM): Shell and soft part morphologies were examined via both light microscopy and SEM, and the radula by SEM alone. Soft parts of two specimens were critical-point dried for SEM studies. For SEM studies of radulae, radular sacs were removed and placed in 10% NaOH solution for 7–8 hours. The radulae were then dehydrated through an ethanol series and laid on a cover slip to air-dry. Samples were coated with gold and examined under a Hitachi S-3400N scanning electron microscope. Type material was deposited at MBMCAS, Qingdao, China.

Molecular Analyses: Five specimens were subjected to molecular analysis. Genomic DNA from each individual was extracted with the Column Genomic DNA Isolation Kit (Beijing TIANGEN, China) according to the manufacturer's instructions. DNA was eluted in elution buffer and stored at −20°C until use. The COI region was amplified by polymerase chain reaction (PCR) using the primers LCO1490 (forward: 5′-GGTCAACAAAT CATAAAGATATTGG-3′) and HCO2198 (reverse: 5′-TTA ACTTCAGGGTGACCAAAAAATCA-3′) (Folmer et al., 1994). PCR reactions were carried out in a total volume of 50 μL, including 2 mL DNA template, 1.5 mM $MgCl_2$, 0.2 mM of each dNTPs, 1 μL of both forward and reverse PCR primers, 10×buffer and 2.5 U Taq DNA polymerase. Thermal cycling was performed under the following conditions: 95°C for 3 min (initial denaturation), followed by 35 cycles of 95°C for 30s (denaturation), 42°C for 30s (annealing), 72°C for 60s (extension) and a final extension at 72°C for 10 min. PCR products were verified on a GelRed-stained 1.5% agarose gel and purified with the Column PCR Product Purification Kit (Shanghai Sangon, China). Purified products were sequenced in both directions using the BigDye Terminator Cycle Sequencing Kit (ver. 3.1, Applied Biosystems) and an AB PRISM 3730 (Applied Biosystems) automatic sequencer. Sequence alignments were generated using Clustal X (Larkin et al., 2007). For phylogenetic analyses, COI sequence from present study and those from GenBank were used (see Table 2). Neighbor-joining (NJ) tree was performed by MEGA 6.06 (Tamura et al., 2013), using Kimura 2-parameter (K2P) model (Kimura, 1980). Bootstrap analyses were performed with 1000 replications.

SYSTEMATICS

Superfamily Neomphaloidea McLean, 1981
Neomphalidae McLean, 1981

Table 2. Works from which the COI sequences derived.

Family	Species	Accession number	Reference
Melanodrymiidae	*Leptogyra inflata*	AB330998.1	Heβ et al., 2008
Melanodrymiidae	*Leptogyropsis inflata*	AB365258.1	Kano, 2008
Melanodrymiidae	*Melanodrymia aurantiaca*	GQ160763.1	Aktipis and Giribet, 2012
Melanodrymiidae	*Melanodrymia aurantiaca*	AB429220.1	Heβ et al., 2008
Neomphalidae	*Cyathermia naticoides*	AY923926.1	Geiger and Thacker, 2005
Neomphalidae	*Cyathermia naticoides*	DQ093518.1	Giribet et al., 2006
Neomphalidae	*Lamellomphalus manusensis*	KY399885	this study
Peltospiridae	*Depressigyra globulus*	AY296825.1	Colgan et al., 2003
Peltospiridae	*Depressigyra globulus*	DQ093519.1	Giribet et al., 2006
Peltospiridae	*Gigantopelta chessoia*	KU312688.1	Roterman et al., 2016
Peltospiridae	*Gigantopelta chessoia*	KU312689.1	Roterman et al., 2016
Peltospiridae	*Nodopelta subnoda*	GU984280.1	Matabos et al., 2011
Peltospiridae	*Nodopelta subnoda*	GU984281.1	Matabos et al., 2011
Peltospiridae	*Pachydermia laevis*	AB429222.1	Heβ et al., 2008
Peltospiridae	*Pachydermia laevis*	GU984266.1	Matabos et al., 2011
Peltospiridae	*Peltospira delicata*	AY923931.1	Geiger and Thacker, 2005
Peltospiridae	*Peltospira operculata*	GU984279.1	Matabos et al., 2011
Peltospiridae	*Peltospira smaragdina*	GQ160764.1	Aktipis and Giribet, 2012
Peltospiridae	*Rhynchopelta concentrica*	GU984283.1	Matabos et al., 2011
Pleurotomariidae	*Bayerotrochus delicatus*	KU759008.1	Zhang et al., 2016

***Lamellomphalus* new genus**

Type Species: *Lamellomphalus manusensis* new species, by original designation.

Diagnosis: Shell haliotiform. Coiled earlier whorl offset to posterior right. Protoconch and first teleoconch whorl with coiling axis parallel to adult aperture. Protoconch surface sculptured with irregular network of low ridges. First 1.2 teleoconch whorl rounded, sculptured with weak axial threads; subsequent teleoconch whorl rapidly expanding, with developed reticulated sculpture. Operculum present, mutispiral with wide free edge. Neck short, dorso-ventrally compressed. Mouth opening triangular; snout apically strongly bilobed and drawn out laterally into points. Cephalic tentacles short, postero-laterally oriented, left tentacle of male greatly enlarged, serving as copulatory organ, deep ventral sperm groove connecting with groove on left side of neck. Epipodial tentacles present posteriorly and laterally. Ctenidium bipectinate, afferent membrane absent; efferent axis merged with floor of mantle cavity by thickened efferent membrane; gill lamellae elongate. Mantle cavity open anteriorly. Radula rhipidoglossate, has a formula of (ca. 10)+4+1+4+ (ca. 10), cusps of inner three lateral teeth similar to those of rachidian teeth with smooth cutting edges, fourth lateral teeth strongly serrate on outer edge; marginal teeth with long, broad shafts, cusp edges deeply divided into about 20 serrations.

Etymology: The name of new genus refers to the lamellae-like structures formed on shell periostracum.

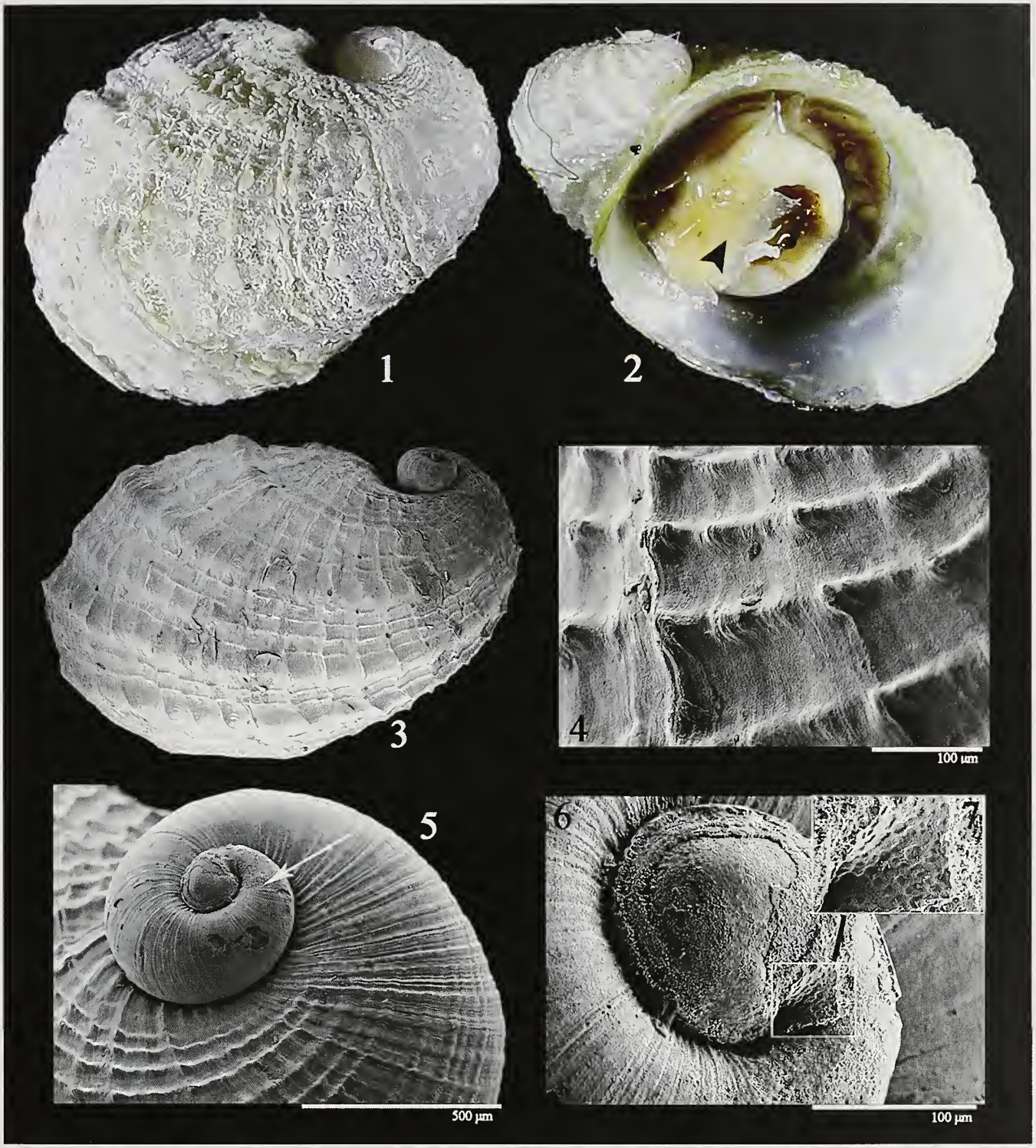
Remarks: *Lamellomphalus* superficially resembles some members Peltospiridae (e.g. *Hirtopelta hirta* McLean, 1989; *Ctenopelta porifera* Warén and Bouchet, 1993, and *Hirtopelta tufari* Beck, 2002) in having haliotiform shell with coiling axis of earlier whorls parallel to final aperture, but differs from them by displaying sexual dimorphism and a copulatory organ, lack of gill afferent membrane and by the non-serrated cusps of the rachidian and lateral teeth. Within Neomphalidae, *Cyathermia*, *Lacunoides*, *Planorbidella*, and *Solutigyra* can be clearly separated from *Lamellomphalus* by their regularly coiled shells. In addition, *Cyathermia* and *Lacunoides* differs from *Lamellomphalus* by having a left tentacle with closed sperm groove and two proximal cirri, and by serration on cusps of rachidian and lateral teeth; *Planorbidella* and *Solutigyra* mainly differ by having cephalic tentacles of equal size in both female and male. *Neomphalus* and *Symmetromphalus* somewhat resemble *Lamellomphalus* in their limpet-shaped shell. However, *Neomphalus* and *Symmetromphalus* can be differentiated from *Lamellomphalus* by having the coiling axis of earlier whorls perpendicular rather than parallel to the adult aperture.

***Lamellomphalus manusensis* new species**
(Figures 1–32)

Description: **Shell** (Figures 1–6) of medium size for family (maximum length 8.9 mm for female and 6.6 mm for male), shell color white. Periostracum olive-green, extending beyond shell margin. Shell haliotiform, profile moderately depressed. Spire small, appressed to the posterior right side of the shell. Protoconch (Figures 5–7) with one rounded whorl, maximum diameter 260 µm, usually heavily eroded, surface sculpture an irregular network of low ridges. Protoconch and first teleoconch whorl with coiling axis parallel to final aperture. Suture deep. First 1.2 teleoconch whorls rounded, sculptured with weak axial threads; subsequent teleoconch whorls rapidly expanding, surface sculpture of radial ribs crossing by thin, curved concentric threads, the two forming sharp nodules on intersections (Figure 4). Radial ribs of varying strengths, primary ones thick, raised, 7–8 in number, each interspace of two adjacent primary ribs with 2–3 secondary ribs. Outline of aperture elongate-oval to nearly rounded, aligned on a single plane or gently arched from side to side. Margin of aperture very thin and fragile, extending into short digitations that correspond to primary radial ribs. Periostracum forming lamellar processes that correspond to intersections of radial ribs and concentric threads.

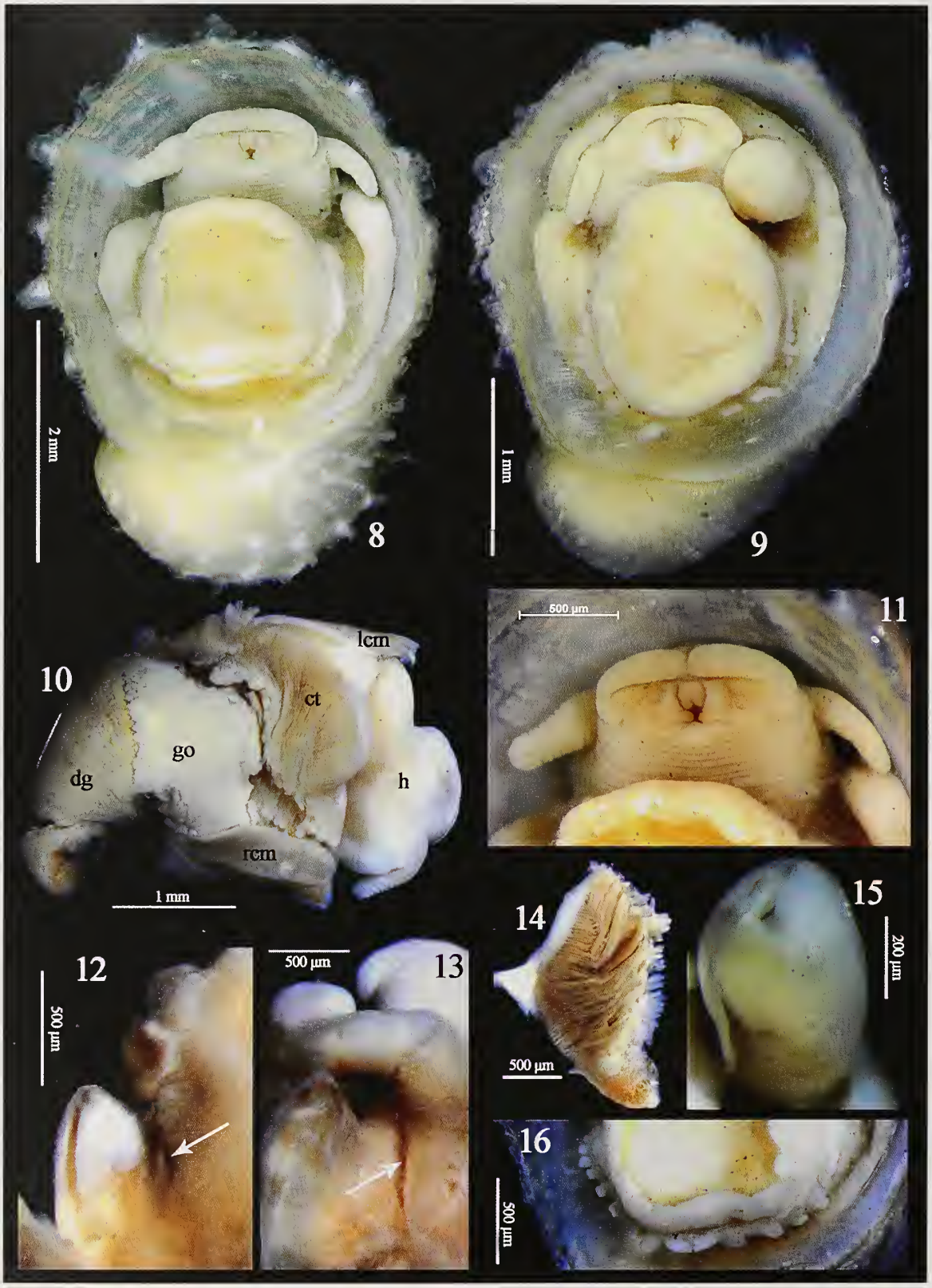
Operculum (Figures 2, 24): Very thin, transparent, attached vertically to posterior region of foot, multispiral, with large, wide final whorl, margin frayed.

External Anatomy (Figures 8–25): Neck short, widened, dorso-ventrally flattened, ventral side with regularly spaced transversal furrows, each side with rounded projection or lobe; males with deep groove on left lateral side, extending to posterior region of mantle cavity; females with short groove (Figures 12, 13). Mouth triangular, perioral area with radial furrows; snout strongly bilobed apically and drawn out laterally into points. Eyes absent. Cephalic tentacles postero-laterally directed, of equal size in female; left tentacle of male very enlarged, relatively thin where attached to head, becoming abruptly thicker distally, about four times as thick as right tentacle, scroll-like in shape, distal end with a seminal opening, ventrally with a deep, open sperm groove that continuous as deep groove on left edge of neck. Mantle skirt very thin. Pallial margin thickened, without papillae, its edge with one dorsal notch, about 3 mm deep. Mantle cavity opened anteriorly, deep and spacious. A pallial vein prominently visible on mantle skirt, originating in right anterior part of mantle skirt and extending posteriorly to end of mantle cavity. Ctenidium enlarged, bipectinate, its large size indicative of filter-feeding, afferent membrane absent; efferent axis arising at posterior of mantle cavity on left, attached to floor of mantle cavity by thickened efferent membrane; gill lamellae elongated and curved, with a blunt pointed

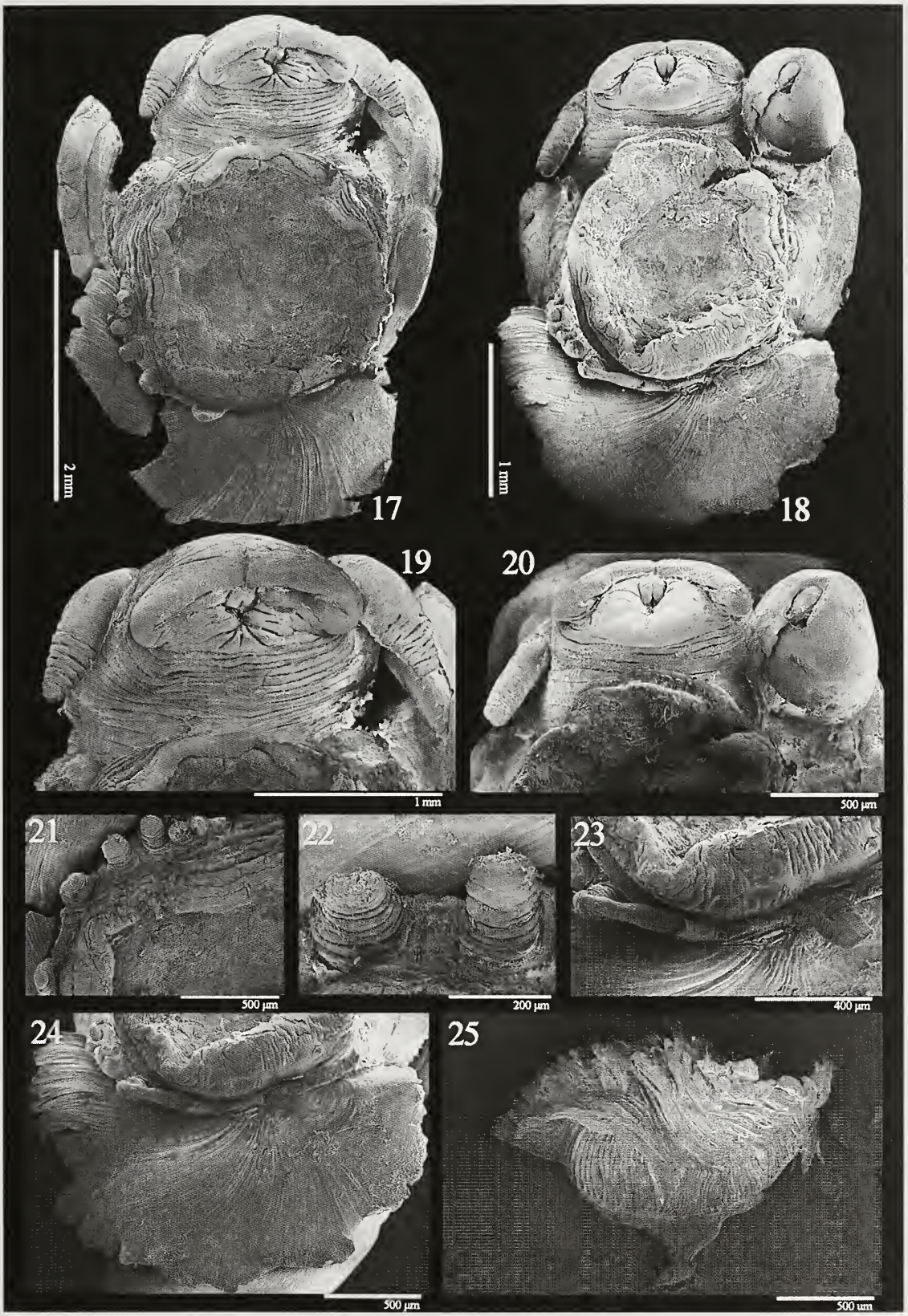


Figures 1–7. Shell of *Lamellomphalus manusensis* new species. **1, 2.** Holotype, length 8.8 mm, black triangle refers to operculum. **3.** Paratype (with periostracum removed), length 6.6 mm. **4.** Sculpture. **5.** Earlier whorls, white arrow indicate protoconch/teleoconch transition. **6.** Protoconch. **7.** Net-like sculpture on protoconch.

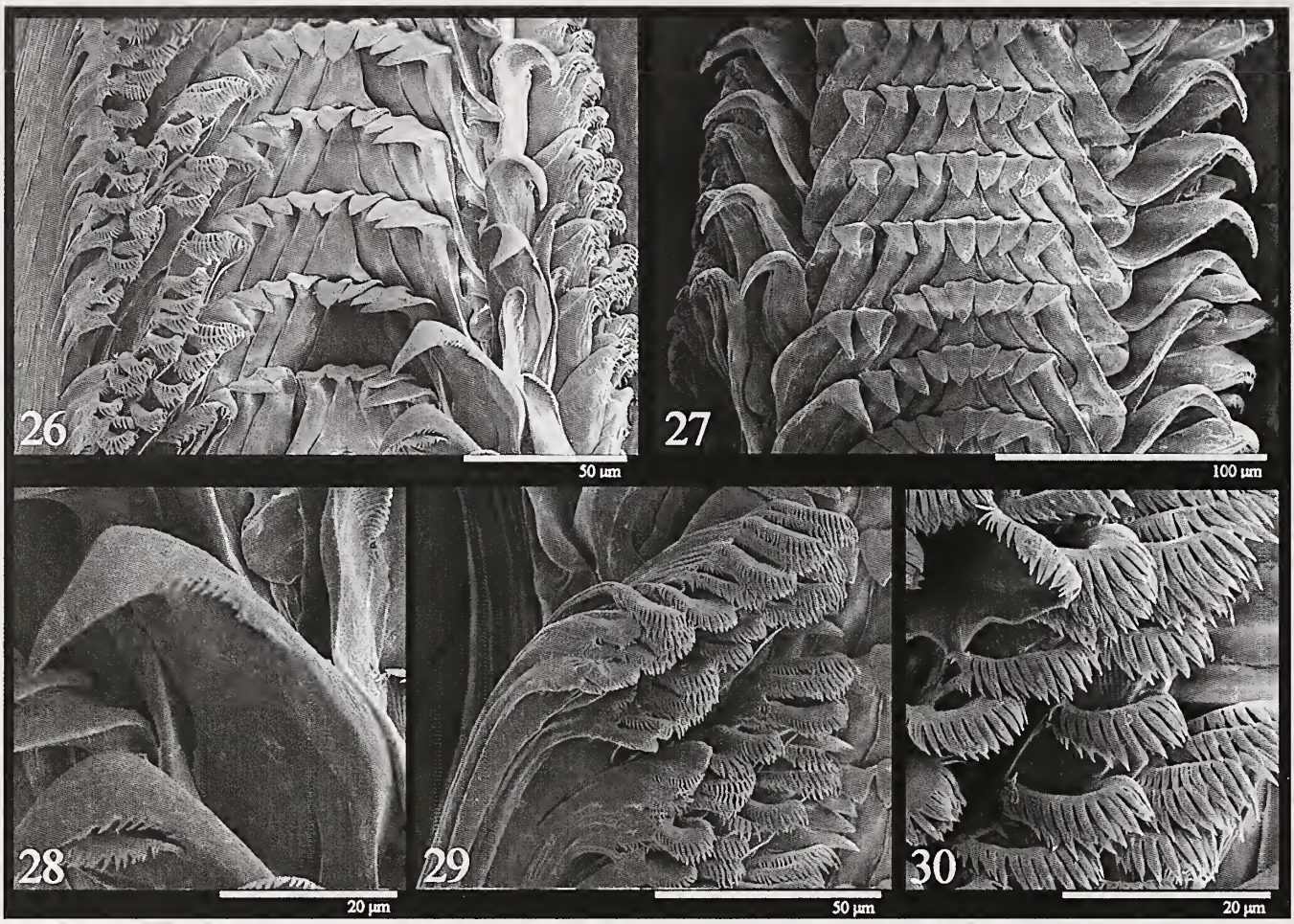
distal end. Columellar muscle horseshoe-shaped, left one long and slender, right one short and broad, both extending anteriorly to middle area of neck. Alimentary groove, or channel, present between right columellar muscle and right neck projection. Gonad located on posterior right, behind right columellar muscle. Pericardium visible as dark structure posterior to gill; ventricle small but solid, rich in brownish pigment, attached on



Figures 8–16. Soft parts of *Lamellomphalus manusensis* new species under light microscope. **8, 9.** Ventral view of animal of female and male, respectively. **10.** Dorsal view of animal (with mantle skirt removed). **11.** Ventral view of head of female; **12, 13.** Left neck portion, white arrows indicate groove on lateral side of female and male, respectively. **14.** Ctenidium. **15.** Left tentacle of male. **16.** Posterior part of foot showing epipodial tentacles. Abbreviations: **ct,** ctenidium; **dg,** digestive gland; **go,** gonad; **h,** head; **lcm,** left columellar muscle; **rcm,** right columellar muscle.



Figures 17–25. Soft parts and operculum of *Lamellomphalus manusensis* new species under SEM. **17–18.** Ventral view of animal of female and male, respectively. **19, 20.** Ventral view of the head of female and male, respectively; **21.** Right lateral epipodial tentacles. **22.** Enlargement of the epipodial tentacles under higher magnification. **23.** Posterior epipodial tentacles. **24.** Operculum. **25.** Ctenidium.



Figures 26–30. Radula of *Lamellomphalus manusensis* new species. **26.** Dorsal view of the radula. **27.** Rachidian and lateral teeth. **28.** Fourth lateral tooth. **29, 30.** Marginal teeth.

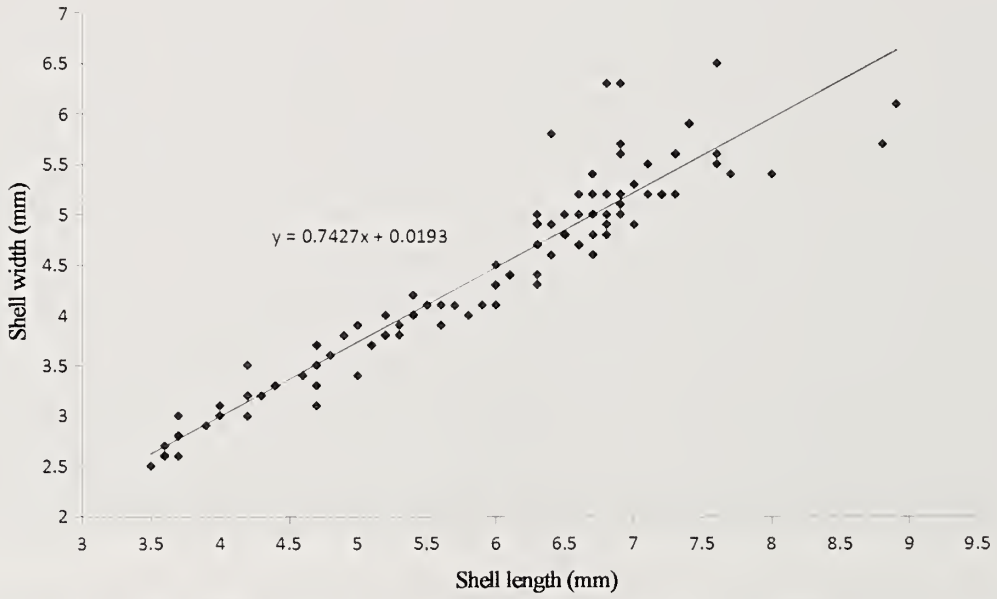


Figure 31. Scatter plot of shell length vs. shell width across the size range of 100 specimens of *Lamellomphalus manusensis* new species.

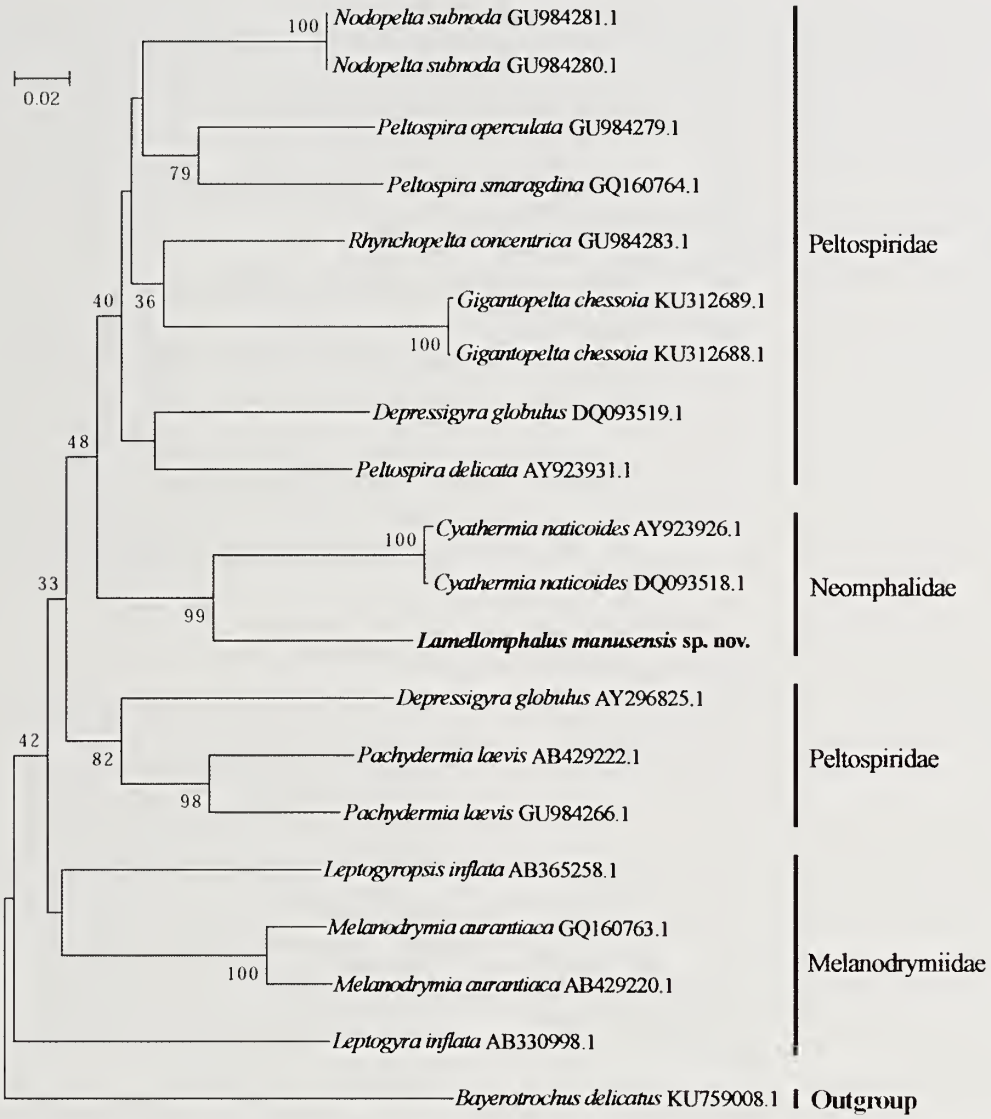


Figure 32. Neighbour-joining tree for Neomphalina based on suitable COI sequences from GenBank and this study. Numbers above branches indicate the bootstrap values.

posterior part of efferent membrane of gill. Foot well developed, rounded, muscular; anterior edge of foot with transverse furrow marking opening of pedal gland. Posterior part of foot encircled by epipodial ridge; epipodial ridge laterally with 4–6 pairs of short, cylindrical epipodial tentacles, posteriorly with one pair of relatively developed ones. Epipodial tentacles becoming smaller anteriorly (Figures 16, 21–23).

Radula (Figures 26–30): Rhipidoglossate, with formula (ca. 10)+4+1+4+(ca. 10). Rachidian teeth and four pairs of lateral teeth of similar morphology. Base of rachidian tooth broad, overhanging moderately long cusp with smooth cutting edges. First to third lateral teeth slightly less prominent than rachidian tooth, innermost bases behind that of adjacent lateral tooth. Fourth lateral tooth with relatively thinner but longer cusp, outer cutting edge serrated. Marginal teeth with long shaft, bearing about 20 long denticles at distal end.

For parameters of shell and scatter plot of shell width against shell length, please see respectively Table 1 and Figure 31.

Type Locality: A hydrothermal vent area at 3°43′ S, 151°40′ E, at depth of 1740 m, Manus Back-Arc Basin.

Type Material: Holotype (registration number: MBM 283053, collection number: M045-1) and about 130 paratypes (registration number: MBM 283054, collection number: M045-2) in MBMCAS. All from type locality, ROV Faxian dive 33, 12 June, 2015.

Distribution and Habitat: Only known from type locality, where they were found on black, hard mineral rock.

Table 3. Pairwise distances among genera of Neomphalina based on Kimura 2-parameter model.

		1	2	3	4	5	6	7	8	9	10
1	*Lamellomphalus*										
2	*Cyathermia*	0.151									
3	*Leptogyropsis*	0.238	0.268								
4	*Melanodrymia*	0.219	0.236	0.203							
5	*Depressigyra*	0.234	0.239	0.216	0.221						
6	*Gigantopelta*	0.248	0.225	0.263	0.252	0.233					
7	*Nodopelta*	0.225	0.197	0.216	0.217	0.185	0.207				
8	*Pachydermia*	0.230	0.221	0.227	0.214	0.191	0.244	0.190			
9	*Peltospiral*	0.214	0.207	0.244	0.224	0.204	0.204	0.154	0.206		
10	*Rhynchopelta*	0.190	0.234	0.208	0.196	0.198	0.170	0.129	0.219	0.170	

Etymology: The name of new species refers to its type locality.

Remarks: Shell surface is covered with a thick olive-green periostracum that extends beyond the shell edge and forms lamellar processes on intersections of radial ribs and concentric threads. This type of periostracum may provide a tighter seal along the shell margin and thus could prevent animal from eventual adverse environmental effects and/or keep potential predators from dislodging the shell from its substrate.

There are some variations in the shape of the aperture, from elongate-oval to nearly rounded, the peristoma aligned on a single plane or gently arched from side to side. As indicated in Figure 31, the ratios shell width: shell length are relatively constant in young snails, but become more variable in adults. We assume that these variations reflect the shape of substratum to which animal need to adapt.

Molecular Analyses: One sequence was obtained for the COI region in *Lamellomphalus manusensis*. The sequence has been deposited in GenBank (Accession number: KY399885). The length of the COI sequence is 629 bp. The Neighbor-joining (NJ) tree (Figure 32) was reconstructed using suitable COI sequences from GenBank and this study. The alignment of COI had a total 437 bp. The NJ tree shows that *Lamellomphalus manusensis* falls into Neomphalidae in which, together with *Cyathermia naticoides* Warén and Bouchet, 1989, it forms a well-supported clade. With available molecular data, the analysis of a 437-bp fragment of the COI gene resulted in 15% pairwise distance between *Lamellomphalus* and *Cyathermia*, whereas the range among *Lamellomphalus* and six genera of Peltospiridae is 19–25% (see Table 3). As COI sequences alone cannot provide sufficient evidence to reflect the familial relationships within this clade, we refrain from discussing any phylogenetic relationships herein. The purpose of the analysis was only to show that *Lamellomphalus* fell into Neomphalidae clade. The phylogenetic relationship of *Lamellomphalus* and other neomphalines needs to be resolved in a multigene phylogenetic study in the future.

DISCUSSION

Based on available morphological information of shell and external anatomy, we placed the new taxon in family Neomphalidae, which confirmed by molecular evidence. Neomphalidae has sexual dimorphism in which the left tentacle in males is modified and serves as a penis, whereas Peltospiridae do not have distinct copulatory organs or modifications of the cephalic tentacles (Fretter, 1989; Israelsson, 1998). In family Neomphalidae, shell shape varies greatly from regularly coiled (*Cyathermia*, *Lacunoides*, *Planorbidella* and *Solutigyra*), to haliotiform (*Lamellomphalus*), to limpet-shaped (*Neomphalus* and *Symmetromphalus*). Thus, *Lamellomphalus manusensis* could be considered as a intermediate form in Neomphalidae. Metapodium with an operculum indicates an incomplete transformation to a limpet-like body plan. These taxa evidently are of common origin, but perhaps underwent a series of divergent evolutionary steps resulting from adaptive radiation. The similarities among *Lamellomphalus* and some peltospirids regarding shell shape, however, should be considered as resulting from convergent evolution.

In addition to the divergent shell morphologies, there is also a wide range of variation in the anatomy among the genera within Neomphalidae, especially in the morphology of the left tentacle in male individuals. *Lamellomphalus manusensis* possesses a postero-laterally oriented, scroll-like left tentacle, with a ventral, open sperm groove and a large proximal seminal opening. However, left tentacles of *Cyathermia* and *Lacunoides* are anterior-laterally directed, have a sausage-shaped distal end, a closed sperm groove, and two prominent proximal cirri; that of *Neomphalus* is posteriorly directed, thick, attached to the neck, tapering to a pointed distal end, and with open sperm groove; that of *Symmetromphalus* is posteriorly directed, sausage-shaped, with dorsal open sperm groove. The left tentacles of species *Solutigyra*

and *Planorbidella* are of equal size in both sexes. The divergent morphologies in left tentacles may have resulted from different reproductive strategies in the adaptive radiations of these different clades to chemosynthetic environments. High levels of plasticity in shell and soft parts morphologies could be one of the reasons for the successful colonization of hydrothermal vents by this group of marine gastropods.

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A remarkable infestation of epibionts and endobionts of an edible chiton (Polyplacophora: Chitonidae) from the Mexican tropical Pacific

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ABSTRACT

Although epibiosis is common in polyplacophorans, we describe an unusual presence of epibionts and endobionts in a single adult specimen of *Chiton articulatus* collected in Guerrero, Mexico, from an eroded habitat of crevices with high wave activity. The epibiont and endobiont specimens covered nearly 90% of the central and lateral areas of the chiton valves while the border of mantle girdle showed no epibiosis. Crustose and filamentous algae, and crustacean arthropods from two common barnacle families, Chthamalidae and Balanidae, represent the observed epibionts. Polychaete (Annelida), bivalve mollusks from two families: Pteriidae (*Pinctada mazatlanica*) and Mytilidae (*Leiosolenus aristatus*), and crustacean arthropods from the burrowing barnacle family Cryptophialidae (*Cryptophialus wainwrighti*) represent the observed endobionts. In addition, finding of *Cryptophialus wainwrighti* represents a new geographic range extension from the type locality in Sinaloa to Guerrero. Epibiosis studies of invertebrates in the intertidal rocky shore, such as the dominant *C. articulatus*, can assist in understanding ecological relationships and patterns of diversity in coastal communities.

Additional Keywords: epibiosis, endobiosis, basibiont, Cirripedia, *Chthamalus* spp., Balanidae, Polychaeta, Bivalvia, *Leiosolenus aristatus*, *Pinctada mazatlanica*, Acrothoracica, *Cryptophialus wainwrighti*

INTRODUCTION

Common in aquatic habitats, epibiosis is the association between a living substrate organism (*basibiont*) and a sessile organism (*epibiont*) attached to the basibiont's outer surface without trophically depending on it (Wahl, 2010). In endobiosis, an organism (*endobiont*) lives under the external surface of its basibiont (Wahl, 1989, 1997; Wahl and Mark, 1999; Trigui El-Menif et al., 2008; Wahl, 2010; see Taylor and Wilson, 2002 for a more complex terminology). In some studies epibiosis is included generally as fouling (e.g., Mendez et al., 2014), biofouling (e.g., El Ayari et al., 2015), or without specific terminology (e.g., Buschbaum et al. 2007).

Epibiosis is found worldwide, especially in marine environments, where any exposed solid surface is likely to be colonized by organisms (Wahl, 1989). Sessile organisms are the major constituents of these communities (Canning-Clode and Wahl, 2010; Mendez et al., 2014). The basibionts more frequently studied are mollusks (Wahl and Mark, 1999; Wahl, 2010), especially those with economic importance such as gastropods and bivalves (e.g., see Table 19.2 in Dürr and Watson, 2010).

Epibiosis has been poorly documented for the class Polyplacophora, where epibionts and endobionts occur in/on the chiton valves. Arey and Crozier (1919) reported adventitious organisms on the dorsal surface of *Chiton tuberculatus* Linnaeus, 1758, including epizoic barnacles and algae, with other organisms living between the algae. Reports of chiton epibiosis have also been represented by pictures, such as in MacGinitie and MacGinitie (1968: 388, fig. 243) where *Mopalia hindsii* is pictured with its valves covered by algae and invertebrates. Bullock and Boss (1971) documented epibiotic calcareous algae, bryozoans, polychaete tubes, and the detrimental endobiont *Leiosolenus aristatus* (Dillwyn, 1817) boring into the valves of *Chiton stokesii* Broderip, 1832, in the southernmost part of the Panamic Province, and *C. tuberculatus*, from the Caribbean. Watters (1981) reported another eastern Pacific mytilid, *Leiosolenus spatiosa* Carpenter, 1857, in the valves of the chiton, *Acanthochitona hirudiniformis* (Sowerby I, 1832). Other epibionts reported on the valves of *Chiton tuberculatus* include species of the sessile barnacle genus *Tetraclita* Schumacher, 1817, calcareous tube-dwelling polychaetes, *Spirorbis* Daudin, 1800 and *Serpula* Linnaeus, 1758, and green algae including *Ulva* Linnaeus, 1753. The algae provide protection for juvenile mollusks, nematodes, archiannelids, and protozoans. Bullock and Boss (1971) did not consider any of the reviewed epibionts to be

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harmful to the host. Phillips (1972) studied the biota on the intertidal chiton *Mopalia muscosa* Gould, 1846, primarily algae and mollusks, and other organisms. Dell'Angelo and Lagni (1980) mentioned an epizoic encrusting bryozoan on the valves of *Chiton olivaceus* Spengler, 1797. While most chiton epibiont and endobiont observations have been made on intertidal and subtidal species, Sigwart (2009a) documented epibiont foraminifers *Hyrrokkin sarcophaga* Cedhagen 1994 on *Leptochiton arcticus* (G. O. Sars, 1878).

The endemic Mexican chiton *Chiton articulatus* Sowerby in Broderip and Sowerby, 1832, is the largest, most abundant, and dominant chiton of the intertidal rocky shore (Galeana-Rebolledo et al., 2014) found along the tropical Pacific coast. It occurs between the states of Sinaloa and Oaxaca, 23°N to 15°N (Ferreira, 1983; Reyes-Gómez and Salcedo-Vargas, 2002; Kaas et al., 2006; Reyes-Gómez et al., 2010). *Chiton articulatus* is used as food, for fish bait, and targeted as an artisanal fishery (García-Ibáñez et al., 2013; Flores-Garza et al., 2012a). It has gained regional importance and economic interest in the southern Mexican Pacific, where restaurants offer it as a gourmet and aphrodisiac item (Ríos-Jara et al., 2006; Avila-Poveda and Abadia-Chanona, pers. observ.). However, it is not currently cultivated and is unregulated by the government.

The aim of this work is to describe the epibionts and endobionts found outside and inside of the valves of a single adult specimen of *Chiton articulatus*, collected in the southern portion of its known area of distribution.

MATERIALS AND METHODS

During one of several campaigns to evaluate the biodiversity of mollusks in the intertidal rocky shores of Guerrero State, Mexico (Galeana-Rebolledo, 2011; Flores-Garza et al., 2012b; Galeana-Rebolledo et al., 2012, 2014), an unusual adult specimen of *Chiton articulatus* was observed to be heavily infested with epibionts and endobionts. The chiton with epibiosis was collected at Ojo de Agua, Guerrero, Mexico (17.300°N, 101.0526°W) from exposed rocks facing the open ocean, where human harvesting would be difficult. The specimen and its epibionts were relaxed following protocols described by Avila-Poveda (2013), fixed with 90% ethanol, and preserved in 70% ethanol. The specimen measured 43.4 mm in length and 32.1 mm in width including the mantle girdle. This corresponds to the adult stage in the species, according to Avila-Poveda and Abadia-Chanona (2013). This specimen was deposited at the Santa Barbara Museum of Natural History (SBMNH), Santa Barbara, California, USA (SBMNH 235597). The epi- and endobionts observed were recorded according to chiton valve number (I–VIII), identified, and deposited at the SBMNH and the Colección Nacional de Crustáceos (CNCR) at the Instituto de Biología of the Universidad Nacional Autónoma de México (IB-UNAM).

RESULTS

The epibionts and endobionts specimens cover nearly 90% of the central and lateral areas of the chiton valves, while the border where the valve had contact with the mantle girdle did not display epibiosis (Figure 1).

Epibionts

The epibionts included two algal morphotypes, one filamentous and the other crustose. Both types were distributed on every chiton valve. Other epibionts were crustaceans, two distinct barnacles, chthamalines and balanids (Figures 1, 12-15), with 26 epibionts in total. All specimens were <4 mm in diameter. The chthamalines (Chthamalidae) were *Chthamalus* Ranzani, 1817 species (Figures 13–14, SBMNH 235604). Also found were six tubiferous, calcareous balanid bases with pores (Balanidae) (Figures 16–17, SBMNH 235609).

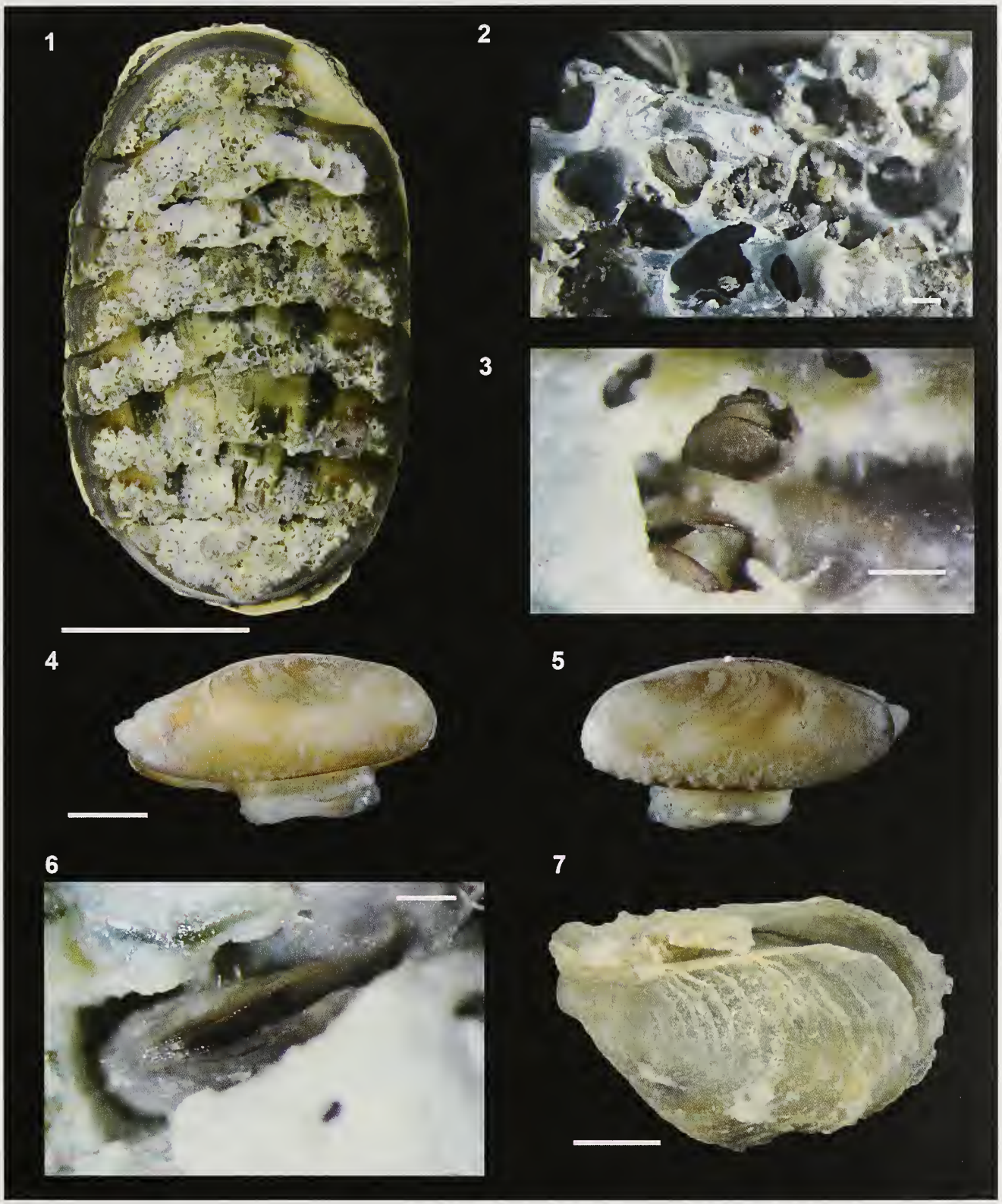
Endobionts

One individual of a free-living polychaete (Annelida) was found in chiton valve VIII. The polychaete could not be identified due to its small size (< 2 mm length) and damage during dissection. Mytilidae endobionts were recorded with 68 individuals of *Leiosolenus aristatus* (Dillwyn, 1817) (Figures 2–5, SBMNH 235588–235594); one *L. aristatus* specimen had perforated the chiton valve, ending just 1–2 mm short of the dorsal musculature. One *Pinctada mazatlanica* (Hanley, 1856) specimen was inside the valve and byssally attached to the chiton valve surface; whereas two *P. mazatlanica* (Figures 6–7, SBMNH 235595–235596) specimens were found deep inside the valves in abandoned boreholes.

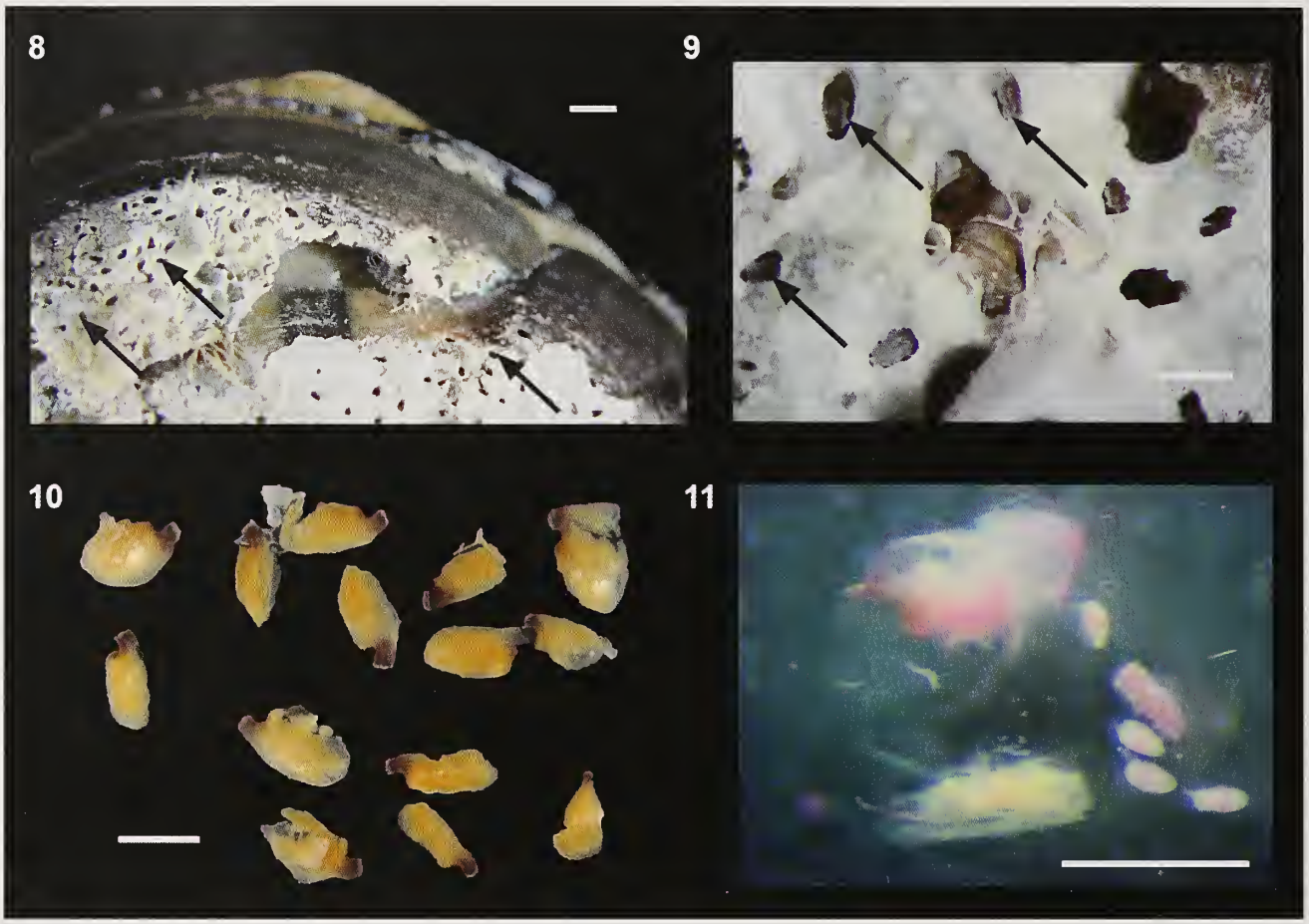
Burrowing acrothoracicans (Cryptophialidae) included 391 *Cryptophialus wainwrighti* Tomlinson, 1969 (Figures 8–11, SBMNH 235599 and 235605 and CNCR 29987). The chiton valves had many small, more or less circular holes on the surface, after dissection of the valves, each hole yielded one *Cryptophialus* female. No minute males were observed. Females, about of 1 mm in length, were apparently brooding embryos, as an opened specimen released four ovoid embryos of cyprids with immature antennules (Figure 11). During dissections (n=4) eggs were observed. The first female had 23 eggs with no eyes, in the second female had 10 eggs with eyes, the third 15 eggs with eyes (Fig. 11), and the last female had no eggs. Eggs with more marked eyes represent the cyprid stage, and during dissections earliest stages with eyes forming were observed, but not any earlier naupliar stages.

Abundance by Chiton Valve

Epibionts and endobionts were present on all eight chiton valves, with 495 individual organisms in total, 6% were epibionts (n=32) and 94% endobionts (n=463) (Table 1). The anterior region, valve I to III, had fewer



Figures 1–7. *Chiton articulatus*. **1.** Dorsal view with numerous juvenile barnacles, largely chthamaline barnacles, plus a few balanid barnacle bases, generally on the eroded valves encrusted and riddled with smaller epibionts. Scale bar = 1 cm. SBMNH 235597. **2.** Mytilid bivalve *Leiosolenus aristatus* boring into valves. Scale bar = 1 mm. **3.** Close up of posterior end of *L. aristatus* in valves. Scale bar = 500 µm. **4, 5.** Right and left lateral views of *L. aristatus*, specimen length 1 mm. SBMNH 235588. **6, 7.** Pteriid bivalve *Pinctada mazatlanica* nestling into old boreholes in valves of *C. articulatus*. Scale bar = 500 µm.



Figures 8–11. *Chiton articulatus*. **8.** Close up of valves showing boreholes (arrows indicating some) of the acrothoracican barnacle, *Cryptophialus wainwrighti*. Scale bar = 1 mm. **9.** Close up of some boreholes showing the opercular bars of the female barnacles (arrows). Scale bar = 500 µm. **10.** Fourteen *C. wainwrighti* females with eggs and developing embryos in their mantle cavities (dark "neck" of sac supporting opercular bars seen in Figure 9, extending toward opening of the burrow). Scale bar = 1 mm. **11.** Partially dissected female with four immature cyprid larvae. Scale bar = 1 mm.

epibionts compared with the central and posterior regions; valve III had the fewest epibiosis (n=34 organisms) in contrast, valve VIII had the greatest (n=117 organisms) (Figure 18).

DISCUSSION

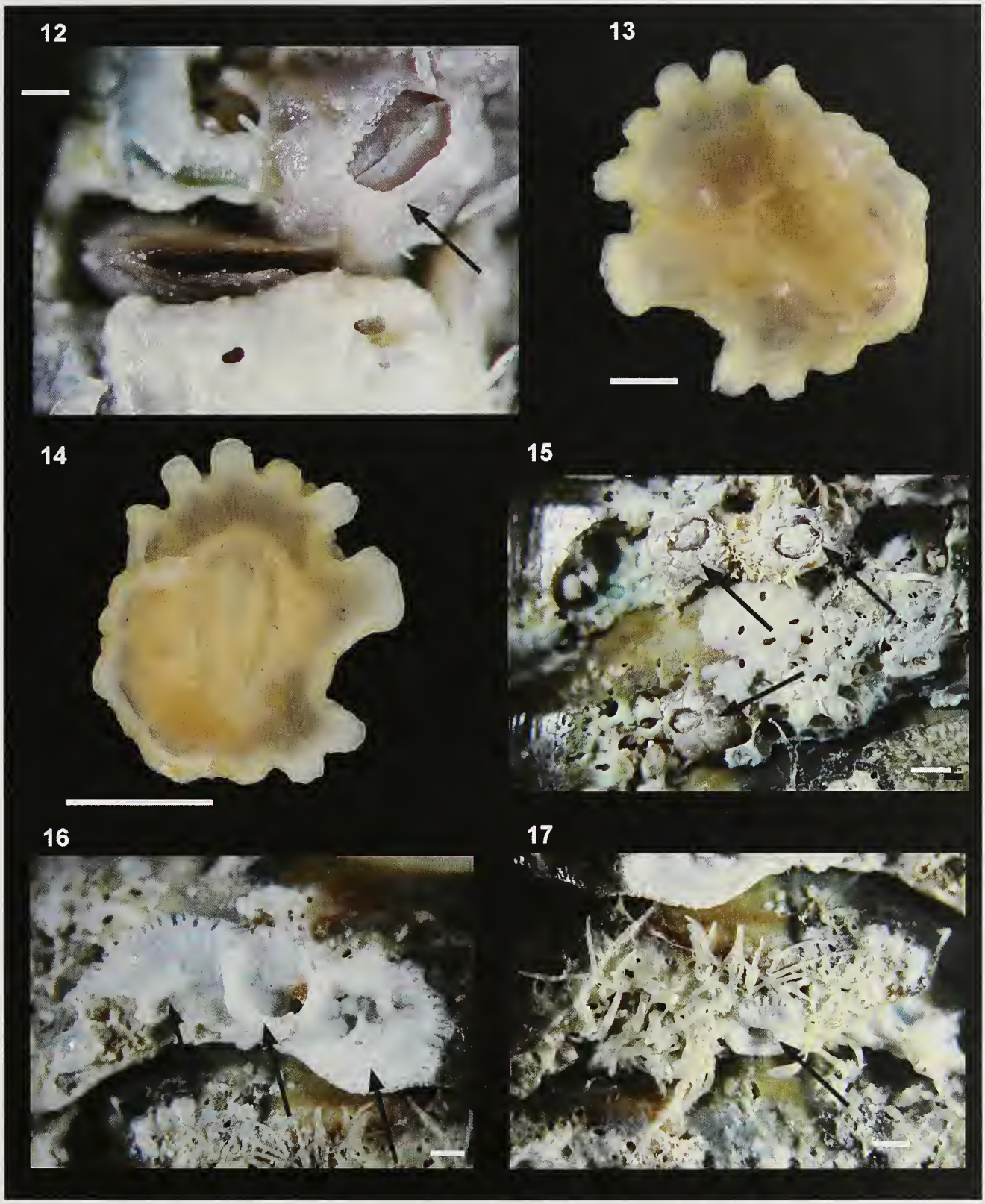
Epibionts

Chthamalines and Balanids: There is uncertainty about the identification of the chthamaline acorn-barnacle epibionts. According to Meyers et al. (2013), there are potentially three species of *Chthamalus* at this latitude. One is a northern species that is more typical of sheltered habitats, *C. southwardorum* Pitombo and Burton, 2007 (according to Newman et al. [2016] proposed name change). The other two are found in wave-exposed habitats, the northern *C. hedgecocki* Pitombo and Burton, 2007 and the southern *C. panamensis* Pilsbry, 1916. However, Chan et al. (2016) restricted the latter to south of 15°N (Tehuantepec), whereby there would be but two species, *C. hedgecocki* from exposed environments and *C. southwardorum* relatively protected ones. While chances are that the juveniles on this chiton were likely the former, the later cannot be ruled out.

Balanid Bases: Likewise, the balanid bases observed could not be specifically identified. The tubiferous calcareous bases with pores found are typical of balanids (Newman and Ross, 1976). However, the bases alone cannot be identified to subfamily, much less generic level, as the specimens were incomplete and some were likely immature. Considering the balanids that are recorded for this area and their characteristics, the bases could be from any one of three of the four subfamilies present in the region: Amphibalaninae Pitombo, 2004, Concavinae Zullo, 1992 and Megabalaninae Newman, 1979.

Endobionts

Polychaeta: Galleries of annelids have also been observed on other chiton species collected along the



Figures 12–17. Balanomorph cirripeds from *Chiton articulatus*. **12.** Chthamaline barnacle, *Chthamalus* sp. (arrow) attached to valve. Scale bar = 500 µm. **13, 14.** Juvenile of *Chthamalus* sp. removed from one valve and photographed from above and below. Scale bars = 500 µm and 1 mm respectively. **14.** Juvenile *Chthamalus* sp. in ventral view. Scale bar = 1 mm. **15.** Balanid barnacles (arrows) attached to valve. Scale bar = 1 mm. **16.** Tubiferous balanid barnacle bases (arrows) on valve II. Scale bar = 500 µm. **17.** Balanid basis (arrow) amongst the algal fronds, between valves II and III. Scale bar = 5 mm.

Table 1. Summary of epibionts and endobionts found, on and in the valves respectively, of a single specimen of *Chiton articulatus*. Valve I (anterior) to VIII (posterior); btb: balanine tuberous bases. All of *Chthamalus* were juvenile of at least two if not three species, *C. hedgecocki*, *C. southwardorum* and *C. panamensis* according to Meyers et al. (2013) or *C. hedgecocki* and *C. southwardorum* according to Chan et al. (2016).

N° of valve	Epibionts		Endobionts	
	N° of organisms	Species	N° of organisms	Species
I	1	*Chthamalus* spp.	4	*Leisolenus aristatus*
			34	*Cryptophialus wainwrighti*
II	3	Balanidae: btb	2	*L. aristatus*
			34	*C. wainwrighti*
III	1	Balanidae: btb	13	*L. aristatus*
	2	*Chthamalus* spp.	18	*C. wainwrighti*
IV	1	Balanidae: btb	7	*L. aristatus*
	4	*Chthamalus* spp.	1	*Pinctada mazatlanica*
			77	*C. wainwrighti*
V	1	Balanidae: btb	9	*L. aristatus*
			1	*P. mazatlanica*
			57	*C. wainwrighti*
VI	9	*Chthamalus* spp.	12	*L. aristatus*
			34	*C. wainwrighti*
VII	5	*Chthamalus* spp.	11	*L. aristatus*
			1	*P. mazatlanica*
			36	*C. wainwrighti*
VIII	5	*Chthamalus* spp.	1	Polychaeta
				L. aristatus
			101	*C. wainwrighti*
Total	32		463	

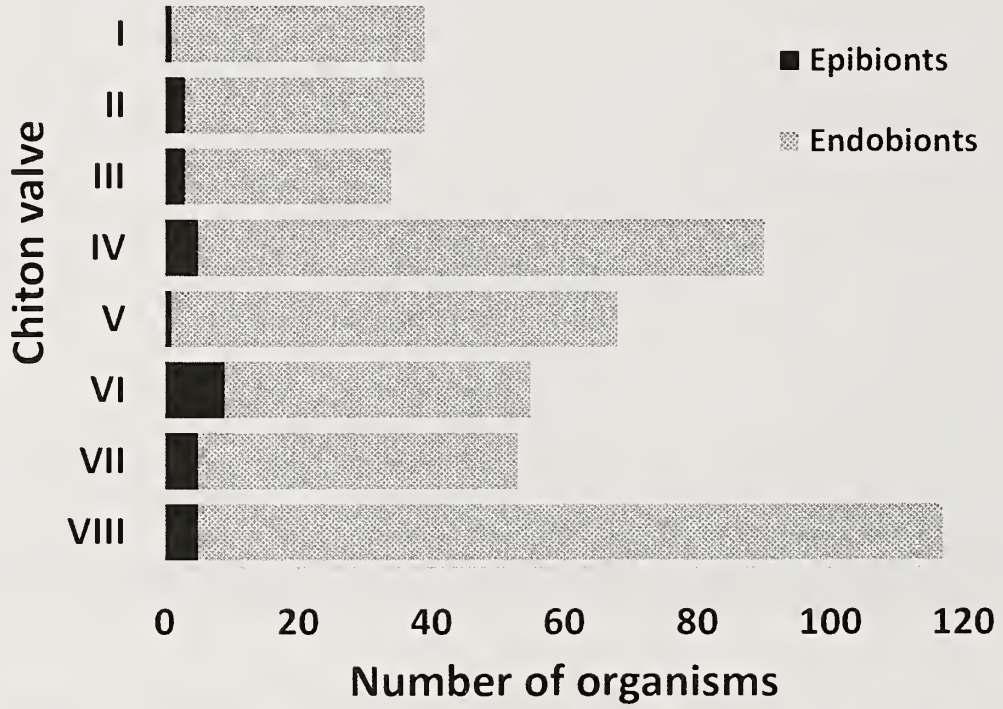


Figure 18. Abundance distribution of epibionts and endobionts by each valve of a single specimen of *Chiton articulatus*. Chiton valves: I, anterior; II–VII, intermediates; VIII, posterior.

coast of Guerrero, including *Chiton albolineatus* Broderip and Sowerby, 1829, *Lepidochitona* sp., *Chaetopleura unilineata* Leloup, 1954, and *Chaetopleura lurida* (Sowerby, 1832). While they have not been studied here, representative specimens are deposited at the Colección Nacional de Moluscos (CNMO) at IB-UNAM.

Leiosolenus aristatus: Bullock and Boss (1971) only found the mytilid bivalve *Leiosolenus aristatus* in "large specimens" of *Chiton stokesii* Broderip in Broderip and Sowerby, 1832 and *C. tuberculatus* (Linnaeus, 1758); these authors did not report the size of chitons. Watters (1981) found *Leiosolenus spatiosus* (Carpenter, 1857) in three chitons of different sizes, all of them seemingly adults. Some reports found chiton epibionts only on larger specimens (Bullock and Boss, 1971; Watters, 1981). In the western Atlantic chiton *Ceratozona squalida* (C.B. Adams, 1845), body size was unrelated to percent cover of epibiotic algae on the girdle (Conelly and Turner, 2009).

Leiosolenus aristatus occurs in warm-temperate to tropical waters in the eastern Pacific, western Atlantic, and eastern Atlantic regions (Valentich-Scott and Dinesen, 2004; Coan and Valentich-Scott, 2012). The species was reported boring in the valves of *Chiton stokesii* and *Chiton tuberculatus*. *Leiosolenus aristatus* bores into calcareous substrates, including the shells of large bivalves (e.g., *Spondylus* Linnaeus, 1758, *Chama* Linnaeus, 1758, *Ostrea* Linnaeus, 1758) and gastropods (e.g., *Haliotis* Linnaeus, 1758, *Patella* Linnaeus, 1758, *Strombus* Linnaeus, 1758, and *Pleuroploca* (P. Fischer, 1884), as well as corals and rocks (Coan and Valentich-Scott, 2012). In the collections of the Santa Barbara Museum of Natural History (SBMNH), *L. aristatus* is present in specimens of *Astraea* Röding, 1798, *Calyptraea* Lamarck, 1799, *Chama*, and *Lottia* Gray, 1833, as well as dead coral (Valentich-Scott, pers. obs. November 2016). It is usually found in shallow water, although Coan and Valentich-Scott (2012) reported shells collected as deep as 300 m. It has recently has been reported from the Mediterranean Sea, boring into shells of the muricid gastropod *Stramonita haemastoma* (Linnaeus, 1767) (El Ayari et al., 2015).

Compared to *Chiton stokesii* and *C. tuberculatus* (data in Bullock and Boss, 1971), the single specimen of *C. articulatus* presented here had more *Leiosolenus aristatus* individuals boring into its valves. It is possible that this could be due to differences in shell hardness and susceptibility for fouling and boring among *C. articulatus* and its congeners. Alternatively, the valve erosion experienced by this chiton specimen might have played a significant role in allowing epibionts to settle. Watters (1981) observed chiton valve erosion was a prerequisite to mytilid boring, and that the boreholes involved the destruction of large portions of both the tegmentum and articulamentum.

Pinctada mazatlanica: This pteriid bivalve is not a borer, but likely uses empty *Leiosolenus* holes as a refuge. *Pinctada mazatlanica* is a large species, reaching a length of 150 mm (Coan and Valentich-Scott, 2012). The bivalves are likely only using the chiton valves as a temporary refuge during a juvenile stage. It is unknown what damage might occur to the chiton, or to the bivalves themselves, as the pteriids continue to grow.

***Acrothoracican* Barnacles:** *Cryptophialus wainwrighti* has been reported from western Mexico (Tomlinson, 1969), found in the marine gastropods *Vasula speciosa* (Valenciennes, 1832) and *Stramonita biserialis* (Blainville, 1832). The only other eastern Pacific species in the genus is its Southern Hemisphere (mostly Chilean) counterpart, *Cryptophialus minutus* Darwin, 1854, which is known to occur within the shells of several mollusks, including *Chiton magnificus* Deshayes, 1827 (Castilla, 2009; Kolbasov, 2009; Pitombo 2010). *Chiton magnificus* is reported to range from Isla San Lorenzo, Peru (12° S) to Tierra del Fuego (55° S), but how much of this remarkably wide range the barnacle occupies is unknown. Another cryptophialid, *Australophialus utinomii* Tomlinson, 1969, attacks the giant chiton, *Dinoplax gigas* Gmelin, 1791 (Chaetopleuridae), from South Africa. Not only are these the only cryptophialid species known to attack chitons, two of them are attacking species of the same genus, *Chiton*. While the known occurrences were noted in Kolbasov (2009), he did not mention chitons in his extended discussion of interactions between acrothoracicans and their hosts. Furthermore, while Yeh et al. (2005) listed 18 chiton species known from Taiwan and nearby islands, one of which is a species of *Chiton*, none of the 18 acrothoracicans from Taiwan reported by Chan et al. (2014), including two species of *Cryptophialus*, are known to attack chitons.

The only other acrothoracican barnacle known from the west coast of Mexico is the lithoglyptid *Kochlorine hamata* Noll, 1872. While previously known from elsewhere in the world, Tomlinson (1969) reports it from Acapulco, Guerrero, Mexico, and in the Gulf of Panama. The burrow opening of this genus differs from that of *Cryptophialus* in being slit-like rather than round or oval and the opercular bars are correspondingly relatively long and fusiform with the sac rather than being supported by an elongate neck. While *K. hamata* is known to attack a wide variety of gastropods as well as coral and at least one balanomorph barnacle, but like most acrothoracicans, it is not known to attack chitons.

Although brooding females of *Cryptophialus wainwrighti* were found, their age is unknown. Utinomi (1961) reported on the development one acrothoracican species, *Berndtia purpurea* Utinomi, 1957. Based on his studies, and that most of the females examined were sexually mature, it could be assumed that the ones in this study were at least a year old. It is possible that the minute males were not observed because they were dislodged during removal of the females from the chiton valves or were left attached to the burrow (Tomlinson, 1969). It is possible that earlier nauplius stages occurred

before hatching while the embryos were still retained within the mantle cavity (Tomlinson, 1969).

Acrothoracican barnacles can be found in large numbers in limestone as well as in basibionts (Kolbasov, 2009). Pitombo (2010) provides good images of the Chilean gastropod *Concholepas concholepas* Bruguière, 1789 riddled with the burrows of *Cryptophialus minutus*. As an example another cryptophialid, *Australophialus melampygos* (Berndt, 1907), is often found infesting the New Zealand abalone *Haliotis iris* Gmelin, 1791. In one case, up to 3350 boring epibionts were recorded in a single shell. *Australophialus melampygos* has also been reported boring into the mussel *Perna canaliculus* (Gmelin, 1791). *Haliotis iris* and *P. canaliculus* are extensively harvested as food sources and the aquacultural environment does not appear to provide a suitable habitat for the recruitment of *A. melampygos*, perhaps because of the poor larval mobility of this species (Batham and Tomlinson, 1965; Webber et al., 2010).

These findings for the distribution of epibionts and endobionts on their basibiont are similar to those of Bullock and Boss (1971), who reported that the posterior edge of the intermediate valves of chitons is usually more eroded in large individuals and thus provide a better substrate for newly settling *Leiosolenus*. Sigwart (2009a) showed that parasitic forams preferentially settled on the posterior valve, apparently because the forams are filter-feeding when they first settle and then transition to a true parasitic lifestyle later in life. In Sigwart (2009b), bryozoan parasites on *Nierstraszella* Sirenko, 1992, had posterior distribution, but among the gills, in the ventral side of the chiton. More epibiosis was recorded on central and posterior region of the chiton (Figure 18).

The bivalves and sessile barnacles on the chiton valves were juveniles. It is not known if they can reach their reproductive state in the limited space on the chiton valve (Bullock and Boss 1971; Watters, 1981). On the other hand, the epibiotic relationship may have potential benefits for barnacles, since their reproductive success relies on the proximity of the mating individuals (Wahl, 1989); the chiton thus may provide a suitable substratum for mating to happen in a suboptimal environment. Although epibionts in other cases may compete with their host for food resources (Wahl, 1989), this does not seems likely to be happening between *Chiton articulatus* and the epibionts and endobionts observed. This species of chiton is a rock-scraping grazer, whereas the barnacles and the bivalves feed on plankton (Celis et al., 2007; Coan and Valentich-Scott, 2012).

Epibiosis in this case not only is likely to result in a loss of functional aesthetes (dorsal chiton valve sensory organs that could have multiple sensory functions, reviewed in Vendrasco et al., 2008) but the action of burrowers (principally *L. aristatus* and *C. wainwrighti*) likely leads to greatly weakened valves (Watters, 1981). Valves also function as an important dorsal armor (Vendrasco et al., 2008). The effects of valve weakening on the behavior of chitons are unknown although it may affect the movement as well as strength of their valves, impairing their resistance to physiological stress during high wave exposure. Chiton defense mechanisms also could be potentially negatively affected, as has been reported for burrowing crabs (Mendez et al., 2014). The epibiosis on chiton valves could be potentially highly detrimental to its normal lifestyle.

While the results presented are from a single specimen, these findings are likely not an isolated case (e.g., Alvarez-Cerrillo et al. 2014; 2016), at least in this chiton species. Epibiosis studies in invertebrates that are dominant and keystone in the intertidal rocky shores as *Chiton articulatus*, could help to understand ecological relationships and patterns of diversity of the coastal community. Finally, this chiton species could serve as a model in quest for answers to different biological, ecological, and fisheries problems involving epi- and endosymbiosis.

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A new species of *Parvaplustrum* Powell, 1951 (Gastropoda: Heterobranchia: Aplustridae) from the northeastern Pacific

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ABSTRACT

A new species of *Parvaplustrum* from the northeastern Pacific, recognized in the literature as undescribed, is formally named herein. This new species is morphologically distinct from the two other species in the genus, *Parvaplustrum tenerum* and *P. japonicum*, and distinguishable by its shell sculpture. The new species is found from Oregon to Baja California, typically associated with chemosynthetic deep-water environments and organic-rich sediments.

Additional Keywords: taxonomy, systematics, shell morphology, chemosynthetic environments

INTRODUCTION

Parvaplustrum Powell, 1951 is a temperate to cold-water genus of aplustrid heterobranch sea slugs. Only two species have been described to date, *Parvaplustrum tenerum* Powell, 1951, from the Falkland Islands, and *Parvaplustrum japonicum* Chaban and Chernyshev, 2013, from the Sea of Japan. A third species from the northeastern Pacific has been cited and discussed in the literature (Cadien, 1995a; Gosliner, 1996; Chaban and Chernyshev, 2013) but never formally named.

In this paper we provide a formal description of this species based on specimens collected from California and Oregon. All the specimens are deposited at the Natural History Museum of Los Angeles County (LACM), the Swedish Museum of Natural History (SMNH), the Department of Invertebrate Zoology and Geology at the California Academy of Sciences (CASIZ) and the Scripps Institution of Oceanography Benthic Invertebrate Collection (SIO).

Family Aplustridae Gray, 1847

Genus *Parvaplustrum* Powell, 1951

Parvaplustrum Powell, 1951: 180.

Type Species: *Parvaplustrum tenerum* Powell, 1951. Falkland Islands, by original designation.

Diagnosis: Shell ovate, globose; sculpture of extremely fine and dense spiral striations. Body with two extensible appendages on each side of headshield; operculum absent; radula with single petaliform lateral tooth in each row, gizzard lacking plates.

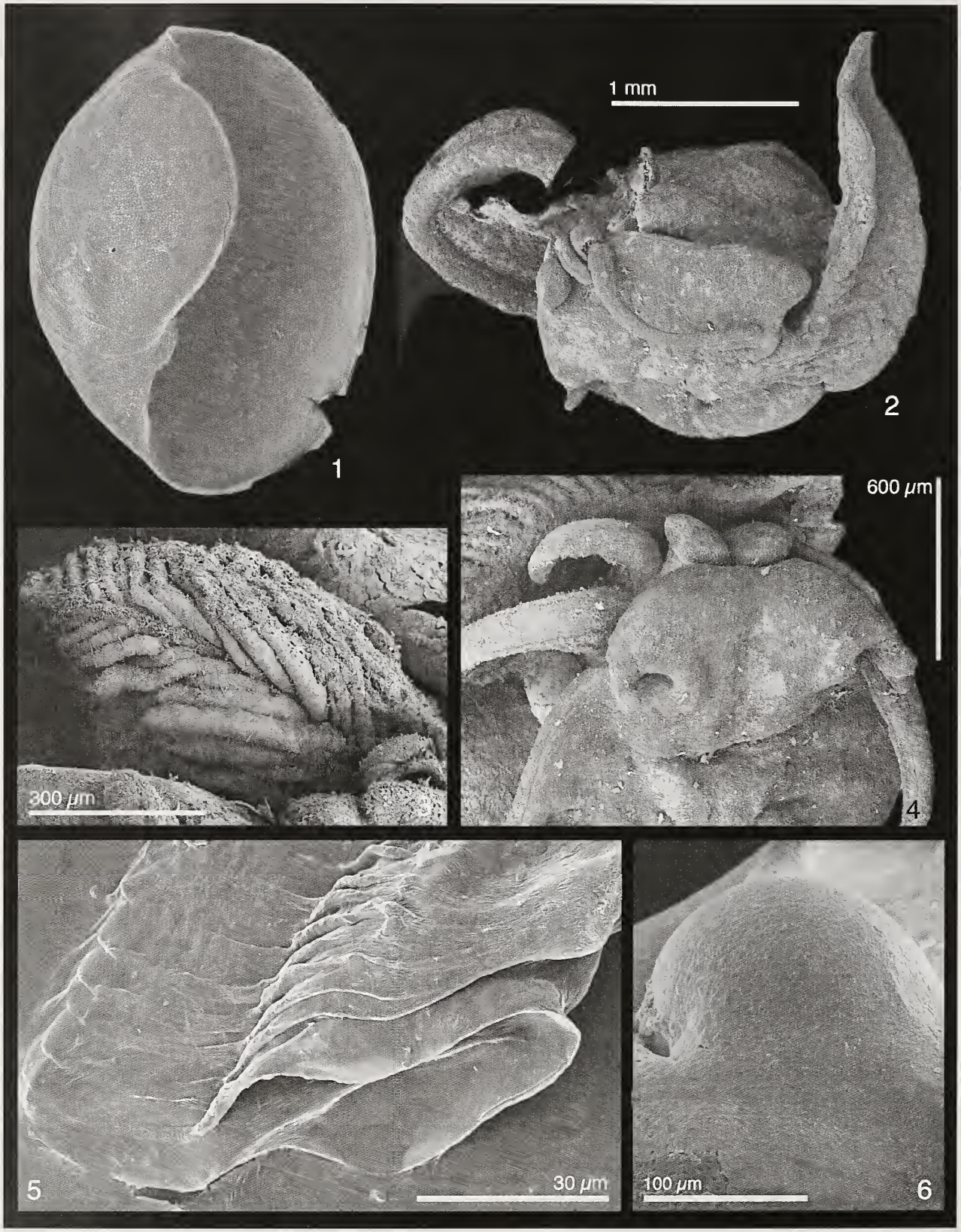
Parvaplustrum cadieni new species

(Figures 1–6)

Parvaplustrum sp. A. Cadien, 1995: [pages unnumbered].
Parvaplustrum sp. Gosliner, 1996: 173, figs. 2.2C–D [as *Parvamplustrum*].

Description: Shell to 2 mm, thin, pyriform (Figure 1). Body whorl slender to very rotund, spire involute, posterior margin of outer forming raised lip. Aperture wide, narrowing slightly mid-length. Sculpture typically absent, with very fine spiral lines of punctuations in larger individuals. Shell color transparent to translucent white. Protoconch located apically on the teleconch, with 1.5 whorls (Figure 6). Animal not examined alive. Preserved specimens with a bifid posterior appendage on each side of headshield (Figure 2). Posterior end of body forming well defined posterior end. Gill plume unipinnate (Figure 3), located above head (Figure 4). Penis elongate, simple. Radula with a single row of petaliform lateral teeth on each side (Figure 5). No jaws were observed.

Type Material: Holotype LACM 3329, 390 m, R/V Velero IV, 17 February 1976, 1 shell specimen, 2.3 mm, from type locality; Paratype CASIZ 216674, off Point Arguello, California, 345 m depth, Santa Barbara Channel Project, Phase I Reconnaissance (Stn. 61), 1 specimen; Paratype SMNH 44660, Hydrate Ridge, off Oregon (44°34′ N, 125°08′ W), 770 m depth, 1999, R/V Sonne Cruise 143 (MUC), 2 specimens.



Figures 1–6. *Parvapustrum cadieni* new species, scanning electron micrographs. **1.** Holotype, 2.1 mm (LACM 3329), off Tanner Bank, California, photo A. Valdés. **2–4.** Details of the external anatomy of a specimen from Oregon (SMNH 44660). **2.** Ventral view. **3.** Gill. **4.** Head (3–4, photos A. Warén). **5.** Radular teeth of a specimen from Oregon (SMNH 44660), photo A. Warén. **6.** Protoconch of a specimen from NW of San Nicolas Island, California (LACM 1995-181), photo A. Valdés.

Type Locality: Off Tanner Bank, California (32°40.97′ N, 119°14.04′ W) (R/V Velero IV, 17 February 1976).

Other Material Examined: SMNH 44675, Hydrate Ridge, off Oregon (44°34.20′ N, 125°08.83′ W), 777 m depth, 11 Aug 1999, R/V Sonne Cruise 148 (MUC90D), 8 specimens; SMNH 45424, subduction zone off the Oregon coast (44°34.19′ N, 125°08.82′ W), 787 m depth, R/V Sonne Cruise 143, 5 specimens; SMNH 45428, subduction zone off the Oregon coast (44°34.20′ N, 125°08.81′ W), 786 m depth, R/V Sonne Cruise 143, 2 specimens; SMNH 111716, Hydrate Ridge, off Oregon (44°34.255′ N, 125°09.289′ W), 809 m depth, DSV Alvin dive 4629, 1 specimen; SMNH 111919, Hydrate Ridge, Off Oregon (44°34.118′ N, 125°09.076′ W), 795 m, DSV Alvin dive 4635, 1 specimen; Hydrate Ridge, off Oregon (44°40.173′ N, 125°05.899′ W), 618 m depth, DSV Alvin dive 4631, 1 specimen; SIO, Hydrate Ridge, off Oregon (44°40.202′ N, 125°05.876′ W), 603 m, DSV Alvin dive 4632, 1 specimen; LACM 1995-181, on a whale skeleton, northwest of San Nicolas Island, California (33°20.35′ N, 119°58.85′ W), 960 m depth, 30 Apr 1995, 6 specimens; LACM 152825, on a whale skeleton, Santa Catalina Basin, California (33°11.72′ N, 118°29.49′ W), 1240 m depth, 14 Oct 1999, DSV Alvin dive 3482, 1 specimen.

Geographic Range: Oregon, possibly from Puget Sound to Bahía Todos los Santos, Baja California (D. Cadien, pers. comm.); 3–809 m.

Biology: Found in chemosynthetic deep-water environments such as cold seeps and whale falls (present paper) as well as organic-rich shelf sediments and deeper portions of bays (D. Cadien, pers. comm.). Specimens as small as 1.1 mm show mature reproductive cells on sectioning, and are assumed reproductively mature (Cadien, 1995).

Etymology: Named in honor of our friend and colleague Don Cadien, who first recognized this species as undescribed.

DISCUSSION

Although tentatively assigned to the family Aplustridae (=Hydatinidae) by Cadien (1995), Gosliner (1996) and Chaban and Chernyshev (2013), the actual phylogenetic position of *Parvaplustrum* remains unknown. Powell (1951) and Marcus and Marcus (1969) suggested that a new family might be needed for this group. Because of the low diversity in *Parvaplustrum* and rarity of all three species, no material available for molecular work has been studied to date. Until such material becomes available, relationships among the species and placement of the genus remain tentative. *Parvaplustrum cadieni* new species is here assigned to *Parvaplustrum* based on the presence of the diagnostic features listed by Chaban and Chernyshev (2013), including an ovate-globose *Haminoea*-like shell without operculum, two extensible appendages on each side of the head shield, radula with a pair of petaliform lateral teeth in a row, and the presence of jaws but not gizzard plates.

As already discussed by Chaban and Chernyshev (2013), *Parvaplustrum cadieni* new species is clearly distinct from the two other known species of *Parvaplustrum*, and the main differences are found in the shell morphology. *Parvaplustrum tenerum* has extremely fine and dense spiral striations, whereas *P. japonicum* has irregularly arranged, numerous, and extremely small pits and *P. cadieni* has spiral lines of punctae. There is also considerable disparity in radular tooth structure among the type species, *P. tenerum*, which has hook-shaped teeth apices (Marcus and Marcus 1969), and the two taxa from the North Pacific, with rounded apices.

A fourth possible species, described as *Meloscaphander* sp. A by Cadien (1995b) has a more globose shell than *P. cadieni*, and is very similar to *P. japonicum*. This undescribed species is typically found in shallower waters, 30–605 m, from Goleta to San Diego, California.

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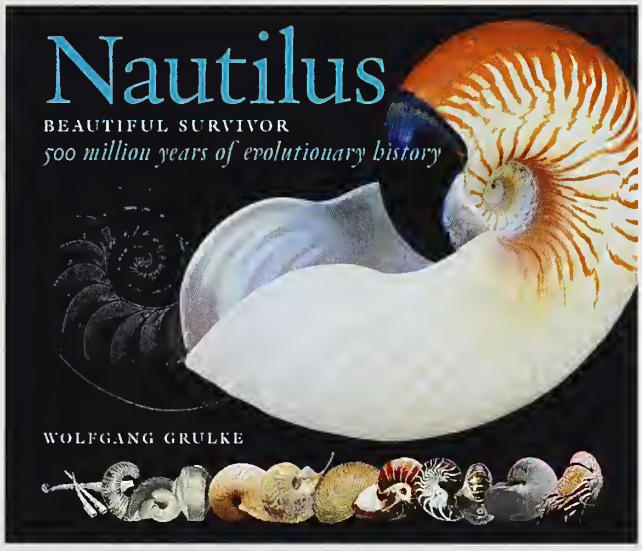
Book Review

Wolfgang Grulke. 2016. **Nautilus: Beautiful Survivor.** At One Communications, United Kingdom, 224 pp., 252×297 mm (landscape format), www.nautilus-thebook.com, ISBN 978-0-9929740-2-2.



Coined in 1834, the term "scientist" at once allowed people who thought they should be taken seriously to distance themselves from less exalted "amateurs". Among scholars of the natural world, however, this distinction has seldom seemed meaningful, and never less so than today, when information belongs to everyone.

A businessman, author and collector extraordinaire, Wolfgang Grulke is an amateur in the original sense of the word: one who loves the study of nature. Many a professional might nevertheless wish to have half his dedication, enthusiasm and resources, which together have produced this unique work.

Within its broad covers an exhaustive review of the morphology, reproduction, feeding, and ecology of all the living *Nautilus* and *Allonautilus* species is accompanied by a detailed history of their discovery and study. Surrounding this core are fascinating vignettes of their roles in native and Western art and culture, from furthest antiquity through the Renaissance, all balanced by a gallery of astonishing Jurassic and Cretaceous specimens from various collections. Throughout the book, high-quality photographs, paintings, portraits, and diagrams place the colorful living animals and their deep blue world among the people whose lives and dreams they have influenced.

Science is nevertheless here in plenty; a chart sets out a revised phylogeny of the entire family, and the accounts of Nautilus biology and ecology are fully up to date. There is a strong conservation message too; the point is well made that, for a multitude of reasons, the Nautiluses today face perhaps the biggest challenge to their survival in their half-billion-year history. In that regard, perhaps the most important aspect of the book is the juxtaposition of ancient species with their contemporary counterparts. "Paleontology" is another venerable term, invented—in 1822—to draw a dubious distinction between the vanished "prehistoric world" and that in which we live today. The two are one and the same, however, and placing Nautiluses preserved in stone alongside their nearly identical living descendants illustrates this in the clearest way. It may just be a happy coincidence that all Nautiluses have recently been classified under Appendix II of the CITES treaty, hopefully granting them some respite.

As in Grulke's previous work "Heteromorph: the Rarest Fossil Ammonites", a firm vision and rigorous attention to detail have ensured that there is none of the poor production and lack of judicious editing that often let down projects of this scale. Every page is carefully laid out and many museums would envy the general sense of coherence that binds together such a broad diversity of images and facts.

In summary, I can think of no better book to use in helping people of any age grasp what "science" actually embodies - a social activity, a way of thinking and above all a holistic world view that balances equally what nature is and what people do. This is definitely a book for the table, not the shelf; opened to any page, it cannot fail to capture the eye and begin conversations.

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Notice

THE 2017 R. TUCKER ABBOTT VISITING CURATORSHIP

The Bailey-Matthews National Shell Museum is pleased to invite applications for the 2017 R. Tucker Abbott Visiting Curatorship.

The Curatorship, established originally in accordance with the wishes of the late Dr. R. Tucker Abbott, Founding Director of the Shell Museum, is awarded annually to enable malacologists to visit the museum for a period of one week. Abbott Fellows are expected, by performing collection-based research, to assist with the curation of portions of the Museum's collection and to provide one talk for the general public. The Museum collection consists of marine, freshwater, and terrestrial specimens. The majority of the collection lots have been catalogued through a computerized database management system; part of the catalogue is already available for searches online at: http://shellmuseum.emc2webs.com/collection/ and via iDigBio at http://ipt.idigbio.org/resource?r=bmnsm-shell. The R. Tucker Abbott Visiting Curatorship is accompanied by a stipend of $1,500.

Interested malacologists are invited to send a copy of their curriculum vitae, a letter detailing their areas of taxonomic expertise and research objectives, and to provide a tentative subject for their talk. Send materials to:

Dr. José H. Leal, Science Director & Curator
The Bailey-Matthews National Shell Museum
P.O. Box 1580
Sanibel, FL 33957 USA
jleal@shellmuseum.org

Applications for the 2017 Visiting Curatorship should be sent electronically to the above e-mail address no later than May 31, 2017, or postmarked by that date if sent by regular mail. The award will be announced by late June 2017. Questions about the Visiting Curatorship should be sent to the e-mail address above, or by phone at:

(239) 395-2233; fax (239) 395-6706

The Delaware Museum of Natural History
is happy to announce and host
the 83rd Annual Meeting of the
American Malacological Society
in Newark, Delaware July 16-21, 2017.

Early registration and abstract submission are open and
reduced rates apply until April 30th.
Please register early!

More information about the meeting, including abstract submission, graduate student travel grants, social events, and the associated iDigBio supported Mollusk Digitization workshop can be found at:
http://www.delmnh.org/ams2017/

Registration for meeting, housing and meals can be accessed at:
https://www.regpacks.com/reg/templates/build/?g_id=100110534

We have two great sessions organized: Mollusks in Peril and Cephalopod Biodiversity, but there is always room for more! If you are interested in planning a session, please get in touch with Liz Shea at eshea@delmnh.org.

Sponsored in part by the State of Florida, Department of State, Division of Cultural Affairs and the Florida Council on Arts and Culture

INSTRUCTIONS TO AUTHORS

THE NAUTILUS publishes articles on all aspects of the biology, paleontology, and systematics of mollusks. Manuscripts describing original, unpublished research and review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of interest to the malacological community will appear in a notices section.

Manuscripts: Each original manuscript and accompanying illustrations should be submitted to the editor preferably via e-mail or as hardcopy in triplicate.

Text must conform to the dimensions of 8½ × 11-inch paper, double-spaced, and single-column throughout (including literature cited, tables, and figure captions). Authors should follow the general recommendations of *Scientific Style and Format—The CSE Manual for Authors, Editors, and Publishers*, available from the Council of Science Editors at www.councilscienceeditors.org. The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Metric, not English, units are to be used. Geochronologic modifiers should be capitalized only when units are formally recognized: for instance, use Late Cretaceous but early Miocene. Likewise, only modifiers of formally recognized chronostratigraphic units are capitalized: use Lower Jurassic but upper Oligocene.

The sequence of sections should be title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). If corresponding author is not the senior author, please indicate. The abstract should summarize in 250 words or less the scope, main results, and conclusions of the article. Abstracts should be followed by a list of additional key words. All references cited in the text must appear in the Literature Cited section and vice-versa. Please follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included within the pagination of cited work. Tables must be numbered and each placed on a separate page. If in doubt, please follow a recent issue of the journal for sequence of sections and other style requirements.

Illustrations: Illustrations are rendered either at full-page width (maximum width 17 cm) or column width (maximum width 8.2 cm). Please take these dimensions into consideration when preparing illustrations. Page-width illustrations ideally should span the entire width of printed page (17 cm). "Tall" page-width illustrations should be avoided, square or "landscape" formats work better. Please design plates accordingly, such that there will be enough space left at the bottom of printed page for plate caption. (Digital technology has made this task much easier.)

All line drawings must be in black, clearly detailed, and completely labeled. Abbreviation definitions must be included in the caption. Line drawings must be high resolution files at least 600 dpi (dots per inch) resolution at actual size. Standard digital formats for line drawings include .tif, .bmp, .psd, .eps, and .pdf.

Photographs may be submitted in black-and-white or color, preferably in RGB mode if in color. Standard digital formats for photographs include .tif, .psd, .jpg, or .pdf. Photographs must be high resolution files at least 300 dpi resolution at actual size.

If more than one figure is included in an illustration, all figures are to be consecutively numbered (Figures 1, 2, 3, . . . , NOT Figures 1A, 1B, 1C, . . . , NOR Plate 1, Figure 1, . . .). In illustrations with more than one figure, make sure that blank areas between figures is kept to a minimum, thereby allowing for more area for each individual figure.

Compressed files (e.g., .jpg) may be used to facilitate transmission of files during original submission, but may not be acceptable at final submission (see below).

Voucher Specimens: Deposition of the holotype in a recognized institutional, public collection is a requirement for publication of articles in which new species-level taxa are described. Deposition of paratypes in institutional collections is strongly encouraged, as is the deposition of representative voucher specimens for all other types of research work.

The Editorial Process: Upon receipt, all manuscripts are assigned a number and acknowledged. The editor reserves the right to return manuscripts that are substandard or not appropriate in scope for THE NAUTILUS. Manuscripts deemed appropriate for the journal will be sent for critical review to at least two reviewers. The reviewers' recommendations will serve as basis for rejection or continuation of the editorial process. Reviewed manuscripts will be sent back to authors for consideration of the reviewers' comments. The revised version of the manuscript may at this point be considered accepted for publication by the journal.

Final Submission: Authors of accepted manuscripts are required to submit a final version via e-mail to the editor at jleal@shellmuseum.org. Please do not send low-resolution or compressed illustration files at this stage. Send any files larger than 20 Mb on a CD or DVD to the editor.

Proofs: After typesetting, proofs will be sent to the author. Author should read proofs carefully and send corrections to the editor within 48 hours. Changes other than typesetting errors will be charged to the author at cost.

Offprints: An order form for offprints will accompany the proofs. Offprints will be ordered through the editor. Authors with institutional, grant, or other research support will be asked to pay for page charges at the rate of $60 per page.

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper)

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